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The origin and identity of invertebrate organisms being transported to Canada's Pacific coast by ballast water

C.D. Levings, J.R. Cordell, S. Ong, and G.E. Piercey

Abstract: We assessed the colonization risk of invertebrate nonindigenous species (NIS) in ballast water being brought into Canada's Pacific coast by indirect and direct methods. Initially we mapped the locations in the northern Pacific Ocean where ships coming into Vancouver Harbour had performed mid-ocean exchange (MOE). Exchange transects (the distance between the start and end positions for the onset and end of MOE) were on average about 400 km long. Samples were also taken from ballast tanks after filling at a northwestern Pacific port and then again after MOE in the mid-Pacific. Invertebrate communities were different pre- and post-MOE, but some coastal organisms were still present after flushing. In addition, samples were obtained from ballast tanks aboard ships in Vancouver Harbour. In "low" salinity samples (<25‰), 13 different taxa were found, and 52 taxa were found in "high" salinity samples (>25‰). Risks could be reduced if MOE was performed in the southerly subtropical domain, south of the subarctic domain and transition zone in the mid-Pacific, or well offshore for north–south shipping routes. For voyages on the west coast of North America, colonization risk of invertebrate NIS is likely higher for ballast water from harbours already colonized by NIS.

Résumé : Nous avons évalué le risque de colonisation par des espèces non indigènes (NIS) d'invertébrés dans les eaux de ballastage apportées sur la côte canadienne du Pacifique par des méthodes directes et indirectes. Au départ, nous avons cartographié les sites dans le Pacifique nord où des navires destinés au port de Vancouver ont opéré un remplacement d'eau de ballastage en mer (MOE). Les transects où ont eu lieu ces remplacements, soit les positions extrêmes des points du début et de la fin de l'opération de remplacement, ont en moyenne 400 km de longueur. Nous avons aussi prélevé des échantillons dans les ballasts après un remplissage dans un port de la côte pacifique du nord-ouest des États-Unis et de nouveau après un remplacement de l'eau (MOE) dans le centre du Pacifique. Les communautés d'invertébrés sont différentes avant et après le remplacement de l'eau, mais il reste encore des organismes des côtes après l'évacuation. De plus, nous avons prélevé des échantillons dans les ballasts de navires dans le port de Vancouver. Nous avons trouvé 13 taxons différents dans les échantillons de « faible » salinité (<25 ‰) et 52 taxons dans les échantillons de « forte » salinité (>25 ‰). Les risque pourraient être minimisés si le remplacement de l'eau de ballastage se faisait dans le domaine subtropical austral, au sud du domaine subarctique et de la zone de transition dans la région centrale du Pacifique, ou encore bien au large des routes de navigation nord–sud. Dans le cas des déplacements le long de la côte occidentale de l'Amérique du Nord, le risque de colonisation par des invertébrés non indigènes (NIS) est vraisemblablement plus élevé lorsqu'on utilise de l'eau de ballastage provenant de ports déjà colonisés par les NIS.

[Traduit par la Rédaction]

Introduction

The maintenance of natural communities and ecosystems is a key goal for marine environmental health, as specified by the Canada Oceans Act. Although the arrival of non-indigenous species (NIS) into the ecosystems of the Great Lakes and the St. Lawrence River estuary via ballast water has been studied for several years (Harvey et al. 1999; Ricciardi 2001; MacIsaac et al. 2002), there are no similar published investigations for Canada's west coast. Numerous NIS have been identified on the coast of British Columbia (B.C.), some likely arrived via ballast water carried by deep-sea ships (Levings et al. 1998, 2002). There are about 20 ports in the B.C. region where deep-sea ships regularly or occasionally visit. After an ocean voyage to B.C., a ship will typically discharge some ballast water off the west coast of Vancouver Island or other locations (e.g., anchorages within the Strait of Georgia) and the rest is discharged in port while loading. Vessels that load in ports without discharging cargo release most of their ballast water into the harbour;

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Gramling (2000) estimated that in Puget Sound, 17% of vessels were of this category. The proportion is likely higher in B.C., especially in Vancouver where large volumes of bulk cargo such as coal and sulfur are loaded. For example, in a 6-month period in 1999, about 4.9 tonnes (t) of ballast water were discharged into Vancouver Harbour (Vancouver Port Authority (VPA), 1900 – 200 Granville Street, Vancouver, BC V6C 2P9, Canada).

Ecological problems relating to ballast water disposal and methods of minimizing the risk of introductions of NIS have been recently reviewed (e.g., National Research Council (NRC) 1996; Ruiz et al. 1997; Kolar and Lodge 2002). As noted by NRC (1996), a ship is a biological island and ballast water is only one habitat for NIS on a ship. Fouling organisms on the hull, sediment in tanks and on anchors, and organisms in sea chests are other vectors for NIS that need consideration. Reductions to ballast discharge are complicated by international shipping and safety concerns, which must be considered in any pragmatic solution to ship-borne NIS risk management.

A widely used short-term method of reducing the risk of accidental introductions by ships' ballast water is mid-ocean exchange (MOE), and this procedure has been adopted by the International Maritime Organization (VPA 2002). MOE is meant to replace coastal organisms in ballast tanks with mid-ocean flora and fauna that are unable to survive in the nearshore environments where they are deposited after deballasting. In the long term, ballast water treatments to inactivate or kill organisms in the water, either when ballast is taken aboard or when it is discharged, may be the preferred method (see Sutherland et al. 2001). Most authorities (e.g., NRC 1996) suggest that ballast water treatment is not a practical solution to the ballast water problem at the present time.

Recent studies have found that organisms continue to arrive by ships' ballast water into B.C. harbours (Levings et al. 1998; Piercey et al. 2000). However, these studies were general surveys, with only a few organisms identified to the species level. Other studies have shown that algae can be grown from water and mud in the bottom of ballast tanks of ships in B.C. harbours (Waters et al. 2001). The recent arrival of the Japanese varnish clam (*Nuttallia obscurata*; Merilees and Gillespie 1995) and the European green crab (*Carcinus maenas*; Jamieson et al. 2002) into B.C. waters in 1991 and 1999, respectively, confirmed that B.C. waters continue to be vulnerable to invasion by potentially hazardous NIS. Although ballast water has not been confirmed as the vector for the green crab, it has been mentioned as a possibility (Jamieson et al. 2002). Approximately 66 nonindigenous invertebrate species have been reported from the Strait of Georgia, which is adjacent to Vancouver Harbour, and it is likely that some of them were transported there by ballast water (Levings et al. 2002).

In this paper, we provide data on the origin and identity of invertebrates from ballast water samples taken before and after MOE and brought to the west coast of Canada. We report data from two empirical studies of ballast water organisms. Samples of ballast water were taken from a ship after ballasting in a port in the northwestern Pacific and then a day after MOE in the mid-Pacific. We also give data on biological samples obtained from ballast tanks aboard ships in Vancouver Harbour. A few of these ships had not performed mid-ocean exchange but most had used empty–refill or flow-through procedure on a trans-Pacific or north–south voyage. To help assess the risk of potential colonization by NIS, we analyzed a geographic data set giving information on where ballast water was exchanged in the northern Pacific Ocean and related these data to the locations of oceanographic domains, their temperature and salinity characteristics, and their endemic fauna, as described in the literature. The ecophysiological features of the endemic fauna from the domains were used to comment on the potential of these species to colonize coastal B.C. waters. We also link the findings to current ballast water management procedures such as the exemptions from the VPA mandatory mid-ocean program (VPA 2002).

Methods

Locations of mid-ocean exchange transects

In 1997, VPA issued Standing Orders (VPA 2002) that stipulate, with some exemptions, that vessels entering the Port of Vancouver must have completed a mid-ocean exchange. When the harbourmaster's staff interviews officers of a vessel about compliance, a suite of data are obtained, including tonnage of ballast water aboard, coordinates of ballasting before MOE, and coordinates of MOE. We analyzed the data obtained to plot the coordinates of the locations where MOE began and ended. Data from 515 interviews on ships that entered Vancouver Port between 7 June and 8 September 1999 were examined. The cruise tracks of the vessels between the beginning and ending of the reported MOE are called exchange transects. The latitudes and longitudes representing the exchange transects were plotted in Arcview geographic information system (GIS). A Pacific-centred view of the world was used as a base map, and a reference grid was manually created and placed over the map of the northern Pacific Ocean.

Mid-ocean exchange: M/S *Skaugran*

Between April and October 1999, biological samples were taken from ballast water aboard the M/S *Skaugran* (hereafter referred to as the *Skaugran*), a cargo vessel (41 905 gross t) involved in trade between North America and Asia and a regular visitor to Vancouver, B.C. During five voyages, nine samples were obtained by engineering staff on the ship after ballasting at six ports in Japan (Appendix A). Eight samples were taken about 24 h after MOE of a ballast tank (200–250 t). MOE took place between 9 and 18 days after the ship left port. It would have been preferable to take repeat samples when the ship arrived in Vancouver, but on these particular voyages, the ship did not travel directly to Vancouver after MOE. The empty and refill exchange procedure was used. Approximate locations for MOE were between 2300 and 3300 km off the Asian coast and further east (Fig. 1). To obtain biological samples, a 12 V electrical diaphragm pump fitted with a 19 mm diameter plastic hose was used to obtain approximately 500 L of ballast water from the ship's standpipes. The hose was lowered about 7.5 m into the tanks. Pumping rate was approximately 17 $L \cdot min^{-1}$. The water was sieved through a 44 μm mesh plankton net in a frame on the

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deck. The material retained on the net was preserved in 5% formalin.

Samples were retrieved from the ship when the vessel arrived in Vancouver. In the laboratory, the samples were decanted through a 37-µm screen, and the remaining material on the mesh was examined using stereo and compound microscopes. Invertebrates were initially sorted into major groups. Copepods were identified to the species level where possible and were the focus of further statistical analyses.

Vancouver Port Authority samples

Sixteen samples of ballast water organisms were obtained from 15 ships in Vancouver Harbour between January and December 2000. Eleven of these ships had completed a voyage from Japan; two provided three samples after voyages from California, one ship had traveled from Mexico, and one from Italy. To collect samples, a 12 V electrical submersible well pump (diameter 38 mm) was connected to Teflon tubing (15 mm diameter) and was lowered about 7.5 m into the ballast tanks. Pumping rate was approximately 11 $L \cdot min^{-1}$. Approximately 200 L of ballast water was sieved through an 80 µm mesh plankton net. Three samples were from ballast water tanks that had not been exchanged, eight were from tanks that had been exchanged by the empty–refill method, three used the flow-through method, and two used a combination of empty–refill and flow-through methods. VPA staff also provided us with sample salinity data obtained with a refractometer. Laboratory methods were as described above for the *Skaugran* samples.

Statistical methods

Paired *t* tests, with Bonferroni adjustment, were used to compare the abundance of specific organisms before and after mid-ocean exchange on the *Skaugran*. A principal component analysis (PCA) using Systat software (Systat Software, Inc., Chicago, Ill.) on invertebrate abundance data from pre- and post-MOE was conducted to investigate differences at the community level. Data were log-transformed ($\log_{10} x + 1$) before analysis of the correlation matrix. Data on unidentified copepod nauplii were removed for the PCA analysis because these organisms were present in large numbers in both pre- and post-MOE samples and could not be identified further. Including these data in the analyses would erroneously suggest that the pre- and post-MOE samples were more similar biologically than they actually were.

Results

Exchange transects

Analyses of the exchange transects (original data shown in National Research Council Data Depository (NRC-DD) Table 1)[2] showed that most exchanges occurred along two major shipping routes: one across the northern Pacific Ocean to Asia (Fig. 1) and another along the west coast of North America (Fig. 2). The trans-Pacific exchange locations were usually at least 1000 km from land, except for the Aleutian Islands. An examination of the data from the west coast of North America showed most of the exchange transects in this area to be within about 500 km of the coastline. In some cases, the transects do not follow a coastline, leading to errors in their position relative to land.

Mid-ocean exchange results from the *Skaugran*

In the pre-MOE samples, 45 copepod taxa were found, with 10 comprising at least 1% of the organisms. In ranked order, these were *Oithona davisae*, unidentified nauplii, *Acartia* (*Acartiura*) *omorii*, *Oithona similis*, *Cyclopina brachystylis*, *Acartia* (*Acartiura*) *hudsonica*, *Pseudodiaptomus marinus*, *Acartia* (*Acartiura*) *longiremis*, *Paracalanus parvus*, and *Halectinosoma* spp. Forty-six copepod taxa were found in the post-MOE samples, but only three taxa comprised at least 1% of the copepods. These were *Oithona similis*, unidentified nauplii, and *Oithona davisae*. Fourteen noncopepod taxa were found in the pre-MOE samples and six in the post-MOE samples. Bivalve veliger larvae accounted for the highest percentage of organisms in the pre-MOE samples, whereas gastropod juveniles dominated the post-MOE samples (NRC-DD Tables 2*a*, 2*b*)[2]. Abundance after MOE was lower than that before MOE for each of the five major copepod groups (calanoids, cyclopoids, poecilostomatoids, harpacticoids, and copepod nauplii) and numerous noncopepod coastal taxa (e.g., polychaetes, cirriped larvae, and bivalve veligers). The difference was least for poecilostomatoids and copepod nauplii. However, there were no significant differences ($p > 0.05$) for each group when tested with paired sample tests using the Bonferroni correction. The ranked *p* values (in parentheses) from the *t* tests comparing pre- and post-MOE abundance were as follows: polychaetes (0.06), calanoids (0.07), harpacticoids (0.11), cirriped larvae (0.30), bivalve veligers (0.34), cyclopoids (0.36), poecilostomatoids (0.54), and copepod nauplii (0.89).

To give an additional perspective on the overall reduction of organisms that may pose an introduction risk, we calculated the mean abundance and percentage pre- and post-MOE for three copepod taxa and three noncopepod coastal taxa as follows: (*a*) two calanoid copepods (*Pseudodiaptomus marinus* and *Acartia* (*Acartiura*) *omorii*); (*b*) a cyclopoid copepod (*Oithona davisae*); (*c*) polychaetes; (*d*) cirriped larvae; and (*e*) bivalve larvae. These copepod taxa are native to the northwestern Pacific but do not occur in or are invasive to the northeastern Pacific. Percentage decreases for the various taxa ranged from 1.0% to 24.1%, with an overall decrease in abundance of 50.9% (Table 1).

PCA analysis and the factor loadings plot of the pre- and post-MOE samples indicate the first two factors accounted for 41.7% of the variance (Fig. 3). To interpret the data, we tabulated the top five dominant taxa within each of the samples (NRC-DD Table 3)[2]. The pre- and post-MOE samples were fairly well separated in the PCA. The groupings in the plot can likely be explained by the presence of two cyclopoid copepod species dominant in the pre- and post-MOE samples: *Oithona davisae* and *Oithona similis*. *Oithona davisae* occurred in seven pre-MOE samples and was the dominant species (>45%) in four. This accounts for the close grouping of samples A5, A6, A7, and A9 in the bottom right quadrant of Fig. 3. *Oithona similis*, an oceanic cyclopoid,

[2] Supplementary data for this article are available on the Web site or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2, Canada. DUD 3542. For more information on obtaining material refer to http://www.nrc-cnrc.gc.ca/cisti/irm/unpub_e.shtml.

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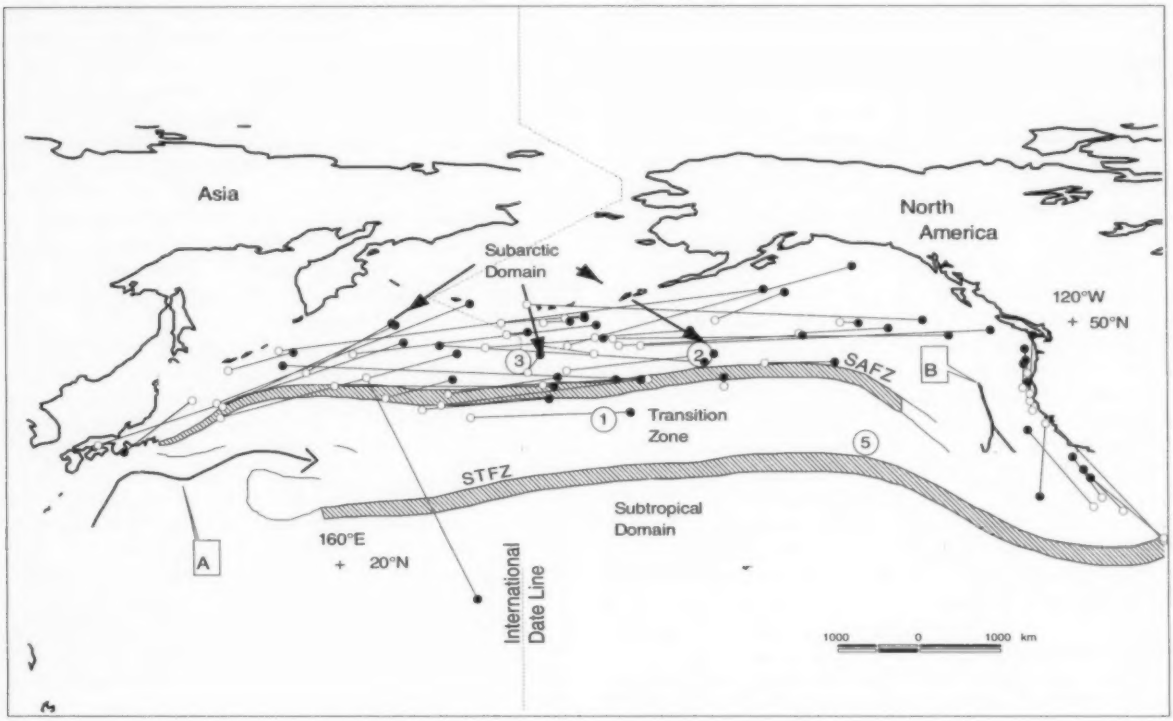
Fig. 1. Positions of exchange transects in the northern Pacific Ocean for a subsample (n = 55) of the ship records analyzed. A, Kuroshio current regime; B, California current system; 1, 2, 3, and 5, positions for mid-ocean exchange (MOE) for the *Skaugran* (see Appendix A); SAFZ, subarctic frontal zone; STFZ, subtropical frontal zone (from Roden 1991); ○, onset of ballast water exchange; ●, termination of ballast water exchange. (Figures showing data for all records analyzed can be found in NRC-DD Figs. 1 and 2; complete tabulation of data is in NRC-DD Table 1.)[2]



was found in all eight of the post-MOE samples. This species was the dominant (>35%) species in six, accounting for the clumping of the post-MOE samples in the upper right quadrant of Fig. 3. An exception to this pattern was post-MOE sample B5 in which *O. davisae* was the dominant species (52%). Data on other copepod taxa also likely contributed to the separation of the samples in the PCA plot. The coastal calanoid copepod *Acartia* (*Acartiura*) *omorii* was a dominant species in five of the pre-MOE samples but was not found in any of the post-MOE samples. Oceanic representatives of the poecilostomatoids were found in six of the eight post-MOE ballast water samples and accounted for between 0.2 and 25.0% of the organisms in these samples. Harpacticoid copepods, a primarily benthic–epibenthic coastal taxon, were found in seven of the pre-MOE samples. The harpacticoids *Ameira* sp. and *Euterpina acutifrons* were among the dominant taxa in samples A1 and A9, respectively. Harpacticoids were also found in four of the post-MOE samples, with *Danielssenia typica* being one of the dominant species in samples B1 and B2 (NRC-DD Table 3)[2].

Noncopepod species from coastal waters were also more abundant in the pre-MOE samples than in the post-MOE samples. This also contributed to the separation of the samples in the PCA plot. Five of the pre-MOE samples contained at least two dominant noncopepod taxa from coastal waters. A total of 13 coastal taxa were found in the pre-MOE samples: polychaetes, cirriped nauplii, cyprids, bivalve veligers, mollusc trochophore larvae, juvenile gastropods, cladocerans, echinoderm larvae, rotifers, nematodes, turbellarians, ascidian tadpole larvae, and mysids (*Acanothomysis aspera*). The post-MOE samples were not dominated by any of these noncopepod coastal taxa; only six different groups were represented in the samples.

A PCA analysis using abundance data from the 15 most abundant taxa in both pre- and post-MOE samples was conducted and showed that the first two factors contributed about 42% of the variance. The relative loadings of the eight calanoids, three cyclopoids, two poecilostomatoids, and two noncopepod taxa in the analyses are shown in Table 2. *Calanus pacificus*, *Ctenocalanus vanus*, *Acartia* (*Acartiura*) *omorii*, damaged calanoid copepodids, *Oithona davisae*, and two noncopepod taxa were among the taxa that showed distinctly contrasting loadings values.

Copepod species after MOE as colonizers

Eleven calanoid, one cyclopoid, five poecilostomatoid, and four harpacticoid taxa were found only in the post-MOE samples. Nineteen copepod taxa were observed in both the pre- and post-MOE samples (NRC-DD Table 4)[2]. A corresponding list showing the reported habitat and distribution of those species identified from the ballast tanks before and after MOE was also developed. Based on their ecophysiological characteristics (primarily temperature and salinity

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Fig. 2. Positions of exchange transects in the northeastern Pacific Ocean for a subsample (n = 11) of the north–south voyages in this region. ○, onset of ballast water exchange; ●, termination of ballast water exchange.

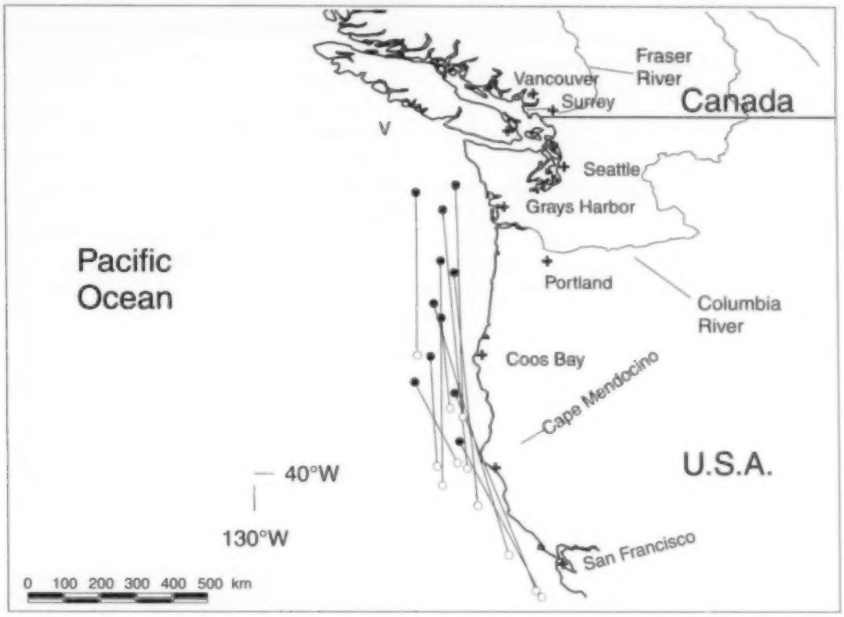

Table 1. Mean abundance (number·m^{-3}) and percentage of total numerical abundance of all organisms for potentially invasive taxa before and after mid-ocean exchange (MOE) on the *Skaugran*.

	Before MOE			After MOE		
	%	Mean	SE	%	Mean	SE
Acartia (*Acartiura*) *omorii* and *Pseudodiaptomus marinus* (combined)	9.7	5 585	3 787	0.1	16	12
Oithona davisae	37.4	21 485	12 862	13.3	2 821	2 776
Polychaeta	3.9	2 210	940	0.1	23	21
Cirripedia larvae	1.1	627	562	0.1	23	21
Bivalvia larvae	12.4	7 109	6 940	<0.1	1	1
Total potentially invasive taxa	64.5	37 016		13.6	2 884	

Note: SE, standard error. Total abundance is based on means.

tolerances, based on range data from the literature (NRC-DD Table 5)[2], we suggest that 10 species of calanoids, three species of cyclopoids, two species of poecilostomatoids, and three species of harpacticoids could colonize B.C. waters (Table 3). Ten of the species have already been reported in B.C.

Samples from ships in Vancouver Harbour

For statistical analyses, samples were divided into those with low salinity (<25‰) and those with high salinity (>25‰). If the salinity of ballast water is >25‰, then the vessel has complied with MOE, according to VPA criteria (VPA 1999).

In the three low-salinity samples, seven major invertebrate groups were found from 13 different taxa (NRC-DD Tables 6*a*, 6*b*)[2]. Calanoids and harpacticoids were found in at least two tanks and accounted for >77% of the total number of individual organisms (Table 4). Mean abundance computed over all organisms was 4768 m^{-3} (standard error (SE) = 1645). The dominant taxa were a calanoid copepod (*Sinocalanus doerri* (mean 1984 m^{-3}, SE = 1621)), the harpacticoid copepod *Tisbe* spp. (mean 1587 m^{-3}, SE = 1587), and the cyclopoid *Limnoithona sinensis* (mean 1018 m^{-3}, SE = 593). These three organisms accounted for 96.3% of the animals in the three samples. The other somewhat less abundant copepods within the low-salinity samples were unidentified species of the calanoids *Diaptomus*, *Sinocalanus*, and unidentified benthic harpacticoids. Other taxa found in the tanks were a flatworm (Platyhelminthes), unidentified decapod larvae, and barnacle nauplii. The vessel from San Francisco (California) had not performed MOE but the ship from Italy had used the empty–refill procedure.

In the 13 high-salinity samples, 23 major invertebrate groups were found, containing 52 different taxa. Calanoids, cyclopoids, poecilostomatoids, harpacticoids, and copepod nauplii were found in at least 46% of the tanks. Cyclopoid copepods accounted for more than 50% of the total number of organisms (Table 4). Mean abundance computed over all organisms was 891 m^{-3} (SE = 343). Ten taxa accounted for at least 1% or more of the organisms. These were *Oithona*

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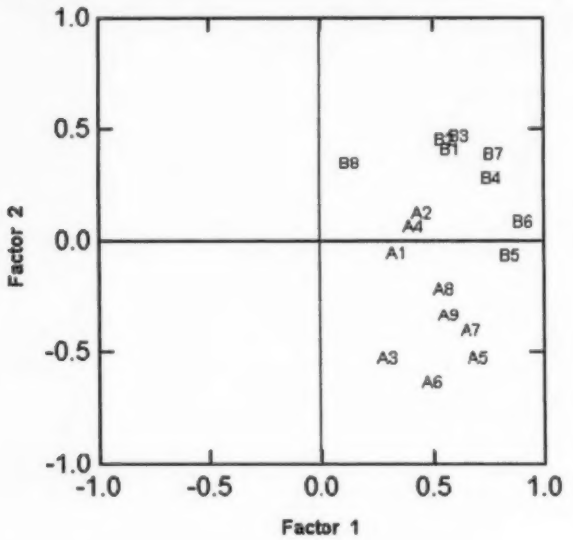
Fig. 3. Principal component analysis on data from pre-MOE (A series) and post-MOE (B series) samples from the *Skaugran*. All faunal data included except copepod nauplii. MOE, mid-ocean exchange.



tenuis, *Oithona* spp., *Oithona oculata*, *Paracalanus parvus*, *Centropages abdominalis*, bryozoan cyphonautes, bryozoan larvae, barnacle nauplii, polychaete larvae, and dinoflagellates. In addition to 33 copepod taxa, 19 other taxa were found. Mean abundance computed over all organisms other than copepods was 143 m^{-3} (SE = 63). Three of the samples (numbers 18, 19, and 20) contained <50 organisms (mean 15 m^{-3}, SE = 8), but abundance in the other 10 samples was higher (mean 1153 m^{-3}, SE = 362). One sample (number 22, arriving from Long Beach, California) was from a ship that had not conducted MOE. This sample contained the most harpacticoids (530 m^{-3}) of the high-salinity ballast water samples (mean 59 m^{-3}, SE = 40).

Discussion

Oceanic ballast water exchange and risk of introduction

Using invertebrates as indicators, our studies in the northern Pacific show that ballast water exchange does not remove all coastal taxa, a finding similar to those of investigators working in other oceans (e.g., Wonham et al. 2001; Taylor et al. 2002). Therefore, it is likely that the ballast water discharged in an arrival port will contain remnant, viable populations of organisms taken up during ballasting in the coastal region of origin. Our post-MOE samples were taken at least 7 days before the *Skaugran* deballasted in a North American port. It is likely that the abundance of some organisms decreased during this final part of the transit, as shown elsewhere (Gollasch et al. 2000; Olenin et al. 2000; Wonham et al. 2001). However, using the rate of population decline over 7 days shown by Wonham et al. (2001) for zooplankton in deck ballast tanks on a trans-Atlantic voyage (their fig. 2*b*), deballasting from the *Skaugran* would have released about 500 cyclopoid copepods·m^{-3}, those remaining from a post-MOE density of approximately 12 000 cyclopoid copepods·m^{-3}. This calculated abundance of cyclopoids immediately before deballasting is also within the range of those observed from the VPA samples (see above). Some of these would likely be coastal species such as *O. davisae*, which was one of the dominant species both before and after MOE in the *Skaugran* samples. This species has already been introduced to San Francisco Bay (Ferrari and Orsi 1984) and was found in the VPA samples.

Table 2. Results of principal component analysis (PCA) with species data from samples from the *Skaugran* before and after mid-ocean exchange.

Taxa	Factor 1	Factor 2
Calanus pacificus	–0.696	0.168
Clausocalanus furcatus	–0.292	–0.101
Ctenocalanus vanus	–0.491	0.238
Eurytemora pacifica	0.448	0.656
Acartia (*Acartiura*) *hudsonica*	0.347	0.730
Acartia (*Acartiura*) *omorii*	0.784	–0.066
Acartia (*Acartiura*) spp.	–0.173	–0.137
Calanoida copepodids, damaged	–0.531	0.357
Oithona davisae	0.538	–0.169
Oithona similis	–0.552	–0.488
Cyclopina brachystylis	0.437	0.549
Oncaea zernovi	0.526	0.481
Clausidiidae (*Hemicyclops*), copepodite stage 1	0.541	0.177
Polychaeta	0.541	–0.289
Bivalvia veligers	0.408	–0.563

Note: Loadings on the first two factors for the 15 most abundant taxa are shown.

The transportation of planktonic organisms by ballast water can only increase their chances of successfully establishing themselves in coastal regions simply by increasing the frequency of inoculation. In our study, we found that post-MOE ballast water contained at least as many copepod taxa as pre-MOE or unexchanged ballast water but had far fewer coastal or nonindigenous taxa. Relative to source or pre-MOE ballast water, post-MOE ballast water therefore has the potential to release at least as many taxa, but likely fewer individuals (e.g., Gollasch et al. 2000) and fewer potentially invasive taxa, into coastal waters. It is difficult to predict the mortality of specific mid-ocean taxa in a ballast tank after MOE, but the premise of MOE is that even if they survive, they will not be viable in coastal waters. However, a central unanswered question about the transport of zooplankton in ship's ballast remains: what is the increased risk of establishment of marine and estuarine NIS when amplified by their ability to withstand changes in temperature and salinity over large ranges (i.e., eurythermal and euryhaline taxa (Chapman 1998; Kolar and Lodge 2002))? Many euryhaline species are known to be able to survive in waters with salinity gradients between 0 and 30‰ (NRC 1996) and have successfully established themselves on the west coast of the United States (Cohen and Carlton 1998).

Although the literature is conflicting (Fager and McGowan 1963; Pickard and Emery 1996; Roden 1991) in terms of the number of water masses or oceanographic domains that exist in the Pacific Ocean and what properties determine their boundaries, in general, the subdivisions have

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Table 3. Habitat or ranges and possible matching of habitat requirements in B.C. waters of copepod species found in *Skaugran* ballast water samples after exchange and before and after exchange.

Taxa	Habitat or range; comments	Match[a]
After exchange only		
Acartia (Acartiura) negligens	Central tropical Pacific, northwestern Pacific, Red Sea	+
Calanus pacificus	Eastern Pacific, Bering Sea	++
Calocalanus pavoninus	Indian Ocean, Brazil; warm water – euryhaline	++
Calocalanus styliremis	Warm water, northeastern Pacific, northwestern Pacific	++
Clausocalanus furcatus	Central tropical Pacific, Mexico, East China Sea	–
Clausocalanus lividus	Northeastern Pacific, Mexico (Pacific); free spawner	++
Clausocalanus mastigophorus	Mexico (Pacific),Taiwan, Brazil	+
Corycaeus agilis	Korea, Taiwan, Japan; open ocean, pelagic	–
Ctenocalanus vanus	Northeastern Pacific, Japan	++
Farranula concinna	Thailand, Galapagos, Japan	–
Farranula gibbula	Thailand, Chile, Japan	–
Macrosetella gracilis	Japan, Taiwan, northeastern Atlantic	+
Microsetella norvegica	Northeast Pacific, Japan	++
Oithona plumifera	Taiwan, Japan, Costa Rica; pelagic, neritic	+
Oncaea media	Japan, Brazil, Mediterranean; neritic	+
Oncaea venusta	Japan; neritic	+
Before and after exchange		
Cyclopina brachystylis	Caroline Islands, Sweden	–
Danielssenia typica	Oregon	++
Oithona davisae	Japan, California	+
Oithona similis	Northeastern Pacific	++
Oncaea dentipes	Brazil, Red Sea, Australia	–
Oncaea zernovi	Japan, Brazil, Adriatic	–
Paracalanus parvus	Northeastern Pacific, Japan, Costa Rica	++
Pseudocalanus newmani	Puget Sound	++
Pseudodiaptomus marinus	Washington, California, Japan; neritic	+

[a]+, the species is a possible survivor if released into B.C. waters; ++, the species is reported from B.C. waters (Mr. S. Romaine, Fisheries and Oceans Canada, Institute of Ocean Science, Sidney, B.C., personal communication); –, possible low recolonization risk of the species if released into B.C. waters.

Table 4. Number of taxa, total abundance (number·m^{-3}), and percent of total abundance of various taxa in high-salinity (H; >25‰, n = 13) and low-salinity (L; <25‰, n = 3) ballast water samples from ships in Vancouver.

	Number of taxa				Total abundance			
	H	H (%)	L	L (%)	H	H (%)	L	L (%)
Calanoida	10	76.9	2	66.7	2260	19.5	6300	44.0
Cyclopoida	8	61.5	2	66.7	5968	51.6	3055	21.4
Poecilostomatoida	9	69.2	3	100	589	5.1	40	0.3
Harpacticoida	7	53.8	3	100	762	6.6	4841	33.8
Copepoda nauplii	6	46.2	0	0	135	1.2	0	0
Cirripidia larvae	4	30.8	1	33.3	402	3.5	15	0.1
Bivalvia larvae	3	23.1	0	0	110	1.0	0	0
Polychaeta larvae	4	30.8	0	0	216	1.9	0	0
Bryozoa larvae	2	15.4	0	0	651	5.6	0	0
Dinoflagellida	2	15.4	0	0	175	1.5	0	0

Note: Only taxa accounting at least 1% of total abundance in "high" salinity samples are shown.

characteristic fauna associated with them. This was supported by the results of our PCA, which suggested that the post-MOE community of organisms was different from the coastal assemblages present before MOE. The major factors responsible for the occurrence of barriers and boundaries are temperature, salinity, and oxygen concentrations, but the divisions can also be a function of currents. The frontal zones between domains are also dynamic and their positions can shift up to 200 km (Roden 1991). Isolation of species within their domains is not therefore absolute. A number of planktonic species are common to two or more domains, and the migration of some species of oceanic plankton into the

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coastal neritic zone is actually a common phenomenon during El Niño events and short-term regime shifts (Mackas et al. 2001). However, these periodic incursions may offer less opportunity for NIS establishment compared with the repeated inoculations from ballast water.

Risks could be further reduced if MOE was performed in the subtropical domain (south of approximately 25°N), south of the subarctic domain and transition zone. This area is characterized by higher salinity and temperature relative to the subarctic domain (>34‰ vs. <34‰; 15–18 °C vs. 5–11 °C, respectively (McGowan and Williams 1973; Thomson 1981)). Different zooplankton and neuston communities are recognized in the two domains (McGowan 1972; Ebberts and Wing 1997; Murphy et al. 1998). The subarctic domain is a location of greater concern for MOE because it extends into the northeastern Pacific and onto the B.C. coast. It follows that species picked up from this oceanic region and discharged into coastal waters may not have barriers to the establishment of populations on the B.C. coast. A second concern is that the subarctic domain maintains a significantly greater standing crop of zooplankton (1000 $mL \cdot m^{-3}$) than water masses further south (McGowan and Williams 1973).

Coastal exchange and risk of introduction

The exchange transects located off the coast of North America were closer to the shore than those in the mid-Pacific Ocean and thus may constitute a greater risk of NIS introduction, with the risk likely decreasing with distance offshore. Coastal water movements on the Pacific coast of North America are complex and complicated by cyclical phenomena such as El Nino events, and it is presently unknown if propagules from intracoastal ballast exchanges are transported onshore and survive. However, San Francisco Bay and other coastal embayments in the region are heavily invaded by both planktonic organisms and those that have no planktonic life history stages (Chapman 1988; Cordell et al. 1992; Cordell and Morrison 1996). As our data show, ships traveling north from California and Mexico can transport large numbers of NIS into B.C. This appears to be similar to intracoastal transport of planktonic organisms on the Atlantic coast of North America, where millions of viable organisms are transported between ports by domestic traffic and pose a potential vector risk (Lavoie et al. 1999). Therefore, intracoastal ship traffic in the northeastern Pacific may pose a significant risk and should be accounted for in regional ballast water regulation. Of particular concern in this regard is the exemption of the VPA Harbourmaster's Standing Orders concerning MOE (VPA 2002). These orders allow that ships with ballast water from north of Cape Mendocino are not required to exchange ballast before discharging in Vancouver. In 2002, about 11% of the ships arriving in Vancouver were from this exclusion zone (VPA 2003) and released unexchanged ballast water. A rationale for the exclusion zone is based on general oceanographic considerations: plankton communities north of Cape Mendocino are considered to be contiguous with those in B.C. waters because of northward-flowing currents (Pickard and Emery 1996). However, this exemption does not take into account transport of NIS among embayments and estuaries. Requiring mandatory MOE for ballast water taken on in ports north of Cape Mendocino could reduce the transfer risk of estuarine and freshwater NIS to B.C ports. Some international shipping ports (e.g., Portland and Coos Bay, Oregon) lie between Cape Mendocino and B.C. and should be considered.

Changes in fauna after ballast water exchange

As mentioned above, the reported efficiency with which coastal taxa are replaced with open-ocean taxa after MOE is highly variable and usually <100% (summarized in Taylor et al. 2002). In a study of mid-ocean exchange efficiency of vessels entering the Great Lakes, between 14% and 33% of the ships contained living freshwater-tolerant zooplankton species in their exchanged ballast (Locke et al. 1991). Ruiz and Hines (1997) reported an efficiency estimate of 90–95% for coastal zooplankton when comparing water from exchanged and nonexchanged ballast tanks on oil tankers in Alaska. Similarly, Wonham et al. (2001) found replacement after MOE of 64–100% of coastal organisms. We could not directly measure exchange efficiency on the *Skaugran* because (*i*) we did not measure mortality or growth of organisms in the 8–15 days between ballasting and exchange, which may have been significant (Gollasch et al. 2000; Olenin et al. 2000); (*ii*) our pump samples were negatively biased toward benthic–epibenthic taxa such as harpacticoid copepods and positively biased toward small planktonic taxa such as cyclopoid copepods; and (*iii*) variation in distribution in the tanks resulting from behaviour (Murphy et al. 2002), ship motion, and tank size were not accounted for in our sampling. However, our data did show a large reduction in the numerical proportion represented by invasive and coastal taxa after MOE on the *Skaugran* — a decrease from 65% to 14%.

One of the challenges of MOE is verification. In B.C., the VPA uses random checks of arriving ballast for benthic harpacticoid copepod presence and abundance as a methodology to help ensure compliance with their mandatory MOE program (VPA 1999), a procedure also suggested by Hay and Tanis (1997). However, as our data show, some harpacticoids remain in the ballast tanks after MOE. This methodology is further complicated by the fact that there are several taxa of cosmopolitan planktonic harpacticoids (Boxshall 1979) that may be confused with coastal–benthic forms by nonspecialists. The VPA also uses 25‰ salinity as a threshold over which it is assumed that MOE had been performed. However, the abundance and diversity of the larvae of nearshore organisms that we found in the high-salinity VPA samples suggests that 25‰ may be too low to use as an indicator (or may also reflect MOE ineffectiveness). A wide range of larvae originating from nearshore species was observed, including cyprid and nauplii stages of barnacles and larval stages of bivalve molluscs, echinoderms, polychaetes, larvaceans, and bryozoans. However, the least diverse sample (sample number 13; six copepod taxa only) was actually from a tank that had not been flushed. The sample was from low-salinity water (6‰). Although the ship's last port of call was San Francisco, the invertebrates in this ship's tanks were dominated by the introduced calanoid copepods *Sinocalanus doerri* and the cyclopoid copepod *Limnoithona sinensis*. Because *Limnoithona sinensis* is now thought to be extirpated from San Francisco Bay (Orsi and Ohtsuka 1999), it is possible that there was remnant estuarine water from another port in this particular tank.

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Five species of copepod recorded from ballast water originating in Japan and sampled in Coos Bay between 1986 and 1991 (Carlton and Geller 1993) were apparently successfully removed from the *Skaugran* tanks during MOE. These were the neritic calanoids *Eurytemora pacifica*, *Acartia* (*Acartiura*) *hudsonica*, *A.* (*Acartiura*) *omorii*, and *A.* (*Acartiura*) *longiremis* and the benthic harpacticoid *Microsetella rosea*. The latter is a cosmopolitan species found in the Atlantic Ocean, Red Sea, North Sea, Mediterranean Sea, Indian Ocean, Caribbean Sea, and Pacific Ocean, including waters off British Columbia (Kask et al. 1982), and was found in *Skaugran* ballast tanks before MOE, but not after. Another harpacticoid, *Zaus caeruleus*, was similarly found only in the *Skaugran* samples taken in the northwestern Pacific, but not in the post-MOE samples. This species also occurs in British Columbia (Kask et al. 1982). Another harpacticoid found by Kask et al. (1982) in waters off British Columbia, *Danielssenia typica*, was found in the *Skaugran* samples from before and after MOE.

Given the present study and others of fauna before and after MOE, it is clear that this procedure usually greatly changes the composition of the fauna in ballast tanks and often reduces NIS. However, some coastal or NIS organisms remain in tanks after MOE, some existing verification protocols are probably ineffective, and intracoastal transport of NIS may be a significant ongoing problem. For these reasons, MOE as it is currently applied on intracoastal and cross-ocean voyages of ships entering British Columbia should be regarded as a temporary method until more effective treatment or exchange protocols are developed.

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Appendix A

Appendix appears on the following page.

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Table A1. Data for ballast water samples taken from the *Skaugran* in six Japanese ports and then after mid-ocean exchange (MOE) in 1999.

Voyage	Sample	Tank filling date	Sampling date for coastal water (pre-MOE)	Location	Tank	Date of MOE	Sampling date for oceanic water (post-MOE)	Sample	Location
1	A1	20 March	20 March	Sendai	#3, wt, ss	5 April	6 April	B2	39°15.3′N, 172°48′E
1	A2	18 March	18 March	Tomakomai	#6, wt, ss	5 April	6 April	B1	39°16′N, 171°28′E
1	A3	25 March	25 March	Hakata	#2, wt, ps	5 April	6 April	B3	39°15′N, 172°06′E
2	A4	9 May	10 May	Tomakomai	#6, wt, ss	24 May	25 May	B5	43°03′N, 165°09′W
2	A6	14 May	14 May	Kawasaki	#4, ts, ss	24 May	25 May	B4	43°15′N, 166°15′W
3	A5	8 July	10 July	Kawasaki	#4, wt, ss	21 July	22 July	B6	42°57′N, 174°30′E
3	A7	11 July	13 July	Nagoya	#2, wt, ss	21 July	22 July	B7	42°52′N, 173°24′W
4	A8	29 August	1 September	Tokyo	#1, wt, ss		–	–	–
5	A9	20 October	20 October	Tomakomai	#5, wt, ps	29 October	30 October	B8	35°46′N, 144°23′W

Note: –, no matching post-MOE sample. Abbreviations: ss, starboard side; ps, portside; tw, topwing; wt, wingtank; ts, topside.

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Trophic structure and energy flow in backwater lakes of two large floodplain rivers assessed using stable isotopes

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Abstract: Carbon and nitrogen stable isotopes ($\delta^{13}C$ and $\delta^{15}N$, respectively) were measured for locally abundant primary producers, detritus, aquatic invertebrates, and fish in backwater lakes of two large floodplain rivers in an effort to understand patterns of energy dependence and trophic structure within these habitats. We observed trophic enrichment values for ^{15}N that were within the ranges observed for other aquatic systems but were often considerably lower than the 3.4‰ typically assumed in stable isotope studies. Production based on benthic and terrestrial material, combined with planktonic production for larval fish, appears to be an important energy source supporting consumers in backwater lakes of large floodplain rivers. Our isotopic data challenge the conventional wisdom that macrophytes are centrally involved in supplying carbon to aquatic consumers in shallow lakes and that food webs in most lakes are sustained almost exclusively by carbon fixed by phytoplankton.

Résumé : Nous avons mesuré les isotopes stables de carbone et d'hydrogène ($\delta^{13}C$ et $\delta^{15}N$) chez les producteurs primaires, le détritus, les invertébrés aquatiques et les poissons communs des lacs situées sur la plaine de débordement de deux grandes rivières dans le but de comprendre les patterns de dépendance énergétique et la structure trophique de ces habitats. Nous avons observé des valeurs d'enrichissement trophique de ^{15}N comprises dans la même gamme que celles des autres systèmes aquatiques, mais ces valeurs étaient souvent considérablement plus faibles que le 3,4 ‰ qu'on assume communément dans les études sur les isotopes stables. Une production basée sur du matériel benthique et terrestre et une production planctonique utilisée par les larves de poissons semblent être les sources d'énergie qui supportent les consommateurs dans ces lacs situés sur les plaines de débordement de grandes rivières. Nos données sur les isotopes mettent en doute la croyance commune que les macrophytes jouent un rôle central dans l'apport de carbone aux consommateurs dans les lacs peu profonds et que les réseaux trophiques de la plupart des lacs sont alimentés par le carbone fixé par le phytoplancton.

[Traduit par la Rédaction]

Introduction

The use of measurements of the natural abundance of carbon and nitrogen stable isotopes ($\delta^{13}C$ and $\delta^{15}N$, respectively) has become common place in assessing energy sources and trophic structure in freshwater food webs (Peterson and Fry 1987; Vander Zanden and Rasmussen 1999). Traditionally, food web structure has been characterized using gut content analysis in combination with field and laboratory observations of feeding. These methods provide information about recent ingestion but not about feeding history and assimilation (Rounick and Winterbourn 1986). Stable isotope analysis has an advantage over traditional techniques in that the $\delta^{13}C$ and $\delta^{15}N$ ratios of a consumer provide a time-integrated measure of assimilated prey, rather than a list of prey items merely encountered in the diet. Specifically, the $\delta^{13}C$ ratio of a consumer reflects (within 1‰) the $\delta^{13}C$ signature of its diet (DeNiro and Epstein 1978; Peterson and Fry 1987), and the $\delta^{15}N$ ratio of a consumer reflects its trophic position because there is an average enrichment of 3.4‰ per trophic level (Minagawa and Wada 1984).

Carbon sources often considered important in lakes include phytoplankton, benthic and epiphytic algae, and aquatic vascular plants (Bunn and Boon 1993; Hecky and Hesslein 1995; Keough et al. 1996). Limnologists often consider feeding pathways derived from phytoplankton to be most important for secondary consumers and fish growth in lakes (Gu et al. 1994; Yoshioka et al. 1994; Gu et al. 1996). Recently, there has been a growing appreciation that benthic primary producers and allochthonous organic matter from ri-

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parian vegetation are also important food resources for invertebrate consumers and fish growth (Hecky and Hesslein 1995; France and Steedman 1996; France 1997). Using stable isotope analysis, France (1997) found that littoral fishes were dependent on terrestrial detritus for part of their energy sustenance in small, oligotrophic lakes. In a review of stable isotope studies performed in tropical, temperate, and arctic lakes, aquatic consumers were nearly equally dependent on benthic algae and phytoplankton (Hecky and Hesslein 1995). Macrophytes and epiphytic algae, a conspicuous and abundant source of fixed carbon in wetlands and shallow lakes, are often thought to be centrally involved in supplying carbon to these food webs (Bunn and Boon 1993). Macrophytes are largely believed to enter the aquatic food web as detritus, rather than through direct herbivory, because of the high content of indigestible organic matter and allelopathic chemicals (Fenchel and Jorgensen 1977; Polunin 1984; Mann 1988). However, several recent stable isotope studies revealed that macrophytes contribute little carbon to aquatic food webs even when they are abundant (Bunn and Boon 1993; Keough et al. 1996; but see Kwak and Zedler 1997).

Backwater lakes form on the floodplain of large river systems as a result of a number of different geomorphological processes (Rosgen 1996). They are typically shallow, experience warmer temperatures, increased residence times, and greater water transparency, and have high rates of biological productivity relative to main channel habitats (Eckblad et al. 1984; Junk et al. 1989). During floods, backwater lakes typically receive inputs of nutrient- and silt-laden water from the river main channel and thus it is unclear whether they function differently from nonfloodplain lakes. Backwater lakes provide important habitat for fish species that prefer low water velocity, as well as seasonal spawning and nursery habitat for other river species (Junk et al. 1989; Scott and Nielson 1989). However, little is known about the contribution to the carbon budget of large river ecosystems of carbon fixed in backwater habitats (Junk et al. 1989). Eckblad et al. (1984) found that in the Mississippi River, invertebrate drift was 10 times higher in side channels that drained backwater areas than in the main channel. Although very few studies have examined the contribution of backwater production to the main stem of large rivers, these studies suggest that backwater habitats may be important contributors of organic matter in these systems (Eckblad et al. 1984).

Potential allochthonous energy sources (i.e., organic matter received from production outside of the system) in backwater lakes could include material deposited during floods or leaf litter falling from adjacent riparian vegetation. Potential autochthonous sources of energy (i.e., organic matter produced within the system) could include production by aquatic macrophytes, phytoplankton, or algae attached to rocks (epilithon), logs (epixylon), and sediments (epibenthic algae). Any of these energy sources may also be linked indirectly to backwater consumers via microbial loops. Little is known about whether autochthonous or allochthonous energy sources drive secondary production in backwater lakes or how energy pathways change seasonally.

In this study, we measured naturally occurring carbon and nitrogen stable isotope ratios of aquatic plants and animals in backwater habitats of the Mississippi and Illinois rivers. Using combined $\delta^{13}C$ and $\delta^{15}N$ signatures, we determined whether organic matter sources (e.g., algae, terrestrial detritus, etc.) could be distinguished from one another at higher trophic levels. We also examined feeding relationships among consumers at higher trophic levels to determine the ultimate sources (producers) from which consumers derive their energy. Finally, we evaluated seasonal and annual differences in the relative importance of energy sources supporting backwater food webs and contrast our results with patterns observed in other lacustrine systems and rivers.

Methods

Study sites and sampling design

We sampled food webs from two backwater lake systems that varied in degree of connectivity to the river channel and presence of macrophytes. Savanna Bay is located in the floodplain of reach 13 (river kilometre (rkm) 867.4 to rkm 872.3) of the Upper Mississippi River in Illinois. It is a 255-ha shallow floodplain lake (mean depth = 1.35 m) with abundant macrophytes that include coontail (*Ceratophyllum demersum*), milfoil (*Myriophyllum* spp.), and pondweeds (*Potamogeton* spp.). Savanna Bay maintains a year-round connection to the main channel on its southwestern shore and is inundated with floodwater during spring flood pulses. Long Lake is a 29-ha shallow floodplain lake (mean depth = 1.35 m) located in the Illinois River floodplain (rkm 14.5 to rkm 17.7). It lacks rooted aquatic macrophytes; however, duckweed (*Lemna* spp.) is prevalent during summer. Long Lake is isolated from the main channel except during flood events.

Food web components sampled

The food web at the backwater sites was assessed in the summer (July) and fall (November) in 1998 and in the spring (early April) and summer (July) in 1999. We sampled primary producers at each site by collecting suspended filamentous green algae and benthic filamentous algae when available. Pure samples were obtained by picking out individual algal filaments. In summer 1999, we also collected epixylon and benthic organic matter to include all food resources thought to be important in these systems. Macrophytes and epiphytic algae were collected when available, and foliage from dominant riparian vegetation was collected from the floodplain forest adjacent to the backwater on all sample dates. Attached algal samples were repeatedly rinsed with distilled water to remove coarse detrital particles; however, a significant biofilm layer likely was still present.

Suspended particulate organic matter (SPOM) was obtained by collecting grab samples of surface water (5–10 L). In the laboratory, particulate organic matter was allowed to settle to the bottom of the container and was collected with a pipette. In summer 1999, we also sampled coarse and fine suspended particulate organic matter (CSPOM, >1.0 mm, and FSPOM, <1.0 mm, respectively) from the water column. FSPOM was further separated into four size fractions: fine particulate organic matter (FSPOM, 250 µm – 1 mm), very fine suspended particulate organic matter (VFSPOM, 64–250 µm), and ultrafine suspended particulate organic matter (two fractions: UFSPOM, 5–64 µm and 0.7–5 µm). Except for UFSPOM, samples were collected for each size fraction by filtering 200 L of surface water through a series of succes-

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sive filters of the appropriate size. UFSPOM was collected by filtering 2–12 L of prefiltered water (64-μm mesh) through either 5-μm Nitex mesh or 0.7-μm glass fiber filter by applying a light vacuum using a perforated porcelain funnel and handheld vacuum pump. After filtering, the particulate material on the mesh was washed into a Ziploc® bag (S.C. Johnson & Son Inc., Racine, Wis.) and placed on ice. All suspended particulate organic matter samples were treated with 1 mol·L^{-1} HCl to prevent carbonate contamination (Angradi 1994).

Macroinvertebrates were collected using a combination of methods. A benthic sweep net (800 μm × 900 μm mesh) was used to obtain macroinvertebrates from the littoral zone, a Ponar grab sampler (Wildco, Buffalo, N.Y.) was used to collect sediments, and a push net (500 μm) was used to sample macroinvertebrates in the water column. All techniques were repeated until a sufficient biomass was obtained (2 mg dry weight per species per sample). Gut contents were removed from all macroinvertebrates by dissection to eliminate bias in the stable isotope signature of the organism due to items in the recent diet (Angradi 1994; Junger and Planas 1994).

Zooplankton were collected by towing a net (64 μm) mounted alongside a boat for 5–10 min. Zooplankton were then placed in Ziploc® bags containing water, and gut contents were allowed to evacuate for 2–3 h while the bags were transported to the laboratory. Samples were then frozen and later separated into taxonomic groups. Zebra mussels (*Dreissena polymorpha*) were collected from rocks in Savanna Bay when water levels were low enough to permit collection (typically summer and fall). No zebra mussels were observed in Long Lake. Only the flesh of zebra mussels was used for analysis because shell material is enriched in ^{13}C and does not reflect what is actually assimilated by consumers (Mitchell et al. 1996).

Larval fish were sampled during the summer sampling periods. They were collected by pushing ichthyoplankton nets (500 μm mesh) mounted to the bow alongside the boat in a direction parallel to shore for 5–10 min. Whole larval fish (minus the gut) were analyzed for stable isotopes. Adult fish were collected from both littoral and open water areas using boat-mounted electrofishing equipment. Several adult fish species were present during all sampling periods, including *Dorosoma cepedianum* (gizzard shad), *Lepomis macrochirus* (bluegill), and *Aplodinotus grunniens* (freshwater drum). During summer, additional fish species included *Ictalurus punctatus* (channel catfish), *Ictiobus bubalus* (smallmouth buffalo), *Cyprinus carpio* (common carp), *Morone chrysops* (white bass), and *Lepisosteus platostomus* (shortnose gar). A filet of dorsal muscle (white muscle) was removed from each fish. These tissues have been shown to be representative of the overall stable isotope signature in fish (Hesslein et al. 1993).

Sample preparation and mass spectrometry

After collection, field samples were placed on ice and transported to the laboratory, where they were either processed immediately or kept frozen for processing later. Samples were sorted, rinsed, and then dried in scintillation vials at 60 °C until they were free of moisture. Samples were then ground into a fine powder using a coffee grinder or metal rod. The grinder or metal rod was dry-wiped clean using extra-lint laboratory wiping tissues to prevent cross contamination between samples.

Mass balance spectrometry was performed on all samples to determine $\delta^{13}C$ and $\delta^{15}N$ ratios. Samples were analyzed using a continuous flow stable isotope mass spectrometer (Micromass; Waters Corp., Milford, Mass.) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108; Thermo Electron Corp., Milan, Italy). Stable isotope ratios are reported in del (δ) units, in parts per thousand (‰) relative to the international standard for that isotope according to the following formula:

$$A_x = \frac{A_x/B_{x\,\text{sample}} - A_x/B_{x\,\text{standard}}}{A_x/B_{x\,\text{standard}}} \times 1000$$

where x is either C or N, A is the heavier isotope, and B is the lighter isotope of the respective element. Isotope ratios for carbon are reported relative to carbon in the Pee Dee limestone deposit, and isotope ratios for nitrogen are reported relative to nitrogen gas in the atmosphere (Peterson and Fry 1987). Analytical precision was ±0.2‰ for carbon and ±0.3‰ for nitrogen, but differences of less than 1‰ were not considered biologically meaningful.

The trophic importance of specific food items to consumers was assessed using a dual isotope approach, taking into account the combined $\delta^{13}C$ and $\delta^{15}N$ ratios of consumers and prey and the fractionation expected to occur for each isotope. We assumed a trophic enrichment of +1‰ for each trophic transfer for $\delta^{13}C$ (DeNiro and Epstein 1978) and +3.4‰ for each trophic transfer for $\delta^{15}N$ (Minagawa and Wada 1984). To assess the trophic enrichment assumption of 3.4‰, we calculated average $\delta^{13}C$ and $\delta^{15}N$ across seasons (fall, spring, and summer) and combined organisms into common feeding guilds. The "source" signature in this analysis was calculated as the average of all sources collected, excluding C_4 plants because previous analyses showed that they were not incorporated into the food web.

Results

Source signatures

Stable isotope ratios for aquatic primary producers in the backwater sites were seasonally dynamic and overlapped the range of $\delta^{13}C$ values for terrestrial C_3 plants (Fig. 1), limiting our ability to distinguish sources of organic matter used by higher trophic levels. In Savanna Bay, most aquatic macrophytes and epiphytic algae had high $\delta^{15}N$ and $\delta^{13}C$ ratios that were distinct from other signatures; however, duckweed (*Lemna* spp.) had $\delta^{15}N$ and $\delta^{13}C$ ratios similar to those of epixylon and SPOM. Suspended filamentous green algae and benthic filamentous algae were enriched in ^{13}C and had $\delta^{15}N$ ratios intermediate to those of C_4 plants and aquatic macrophytes (Fig. 1*a*), but these two algae were not well separated from each other. SPOM and UFSPOM (generally assumed to be composed primarily of phytoplankton in lakes) were poorly separated (both $\delta^{13}C$ and $\delta^{15}N$) from epixylon in summer and from terrestrial C_3 plants in all seasons ($\delta^{13}C$).

Long Lake lacked macrophytic vegetation except for duckweed. This system had a smaller range in algae $\delta^{13}C$ and $\delta^{15}N$ and higher overlap between attached algal and

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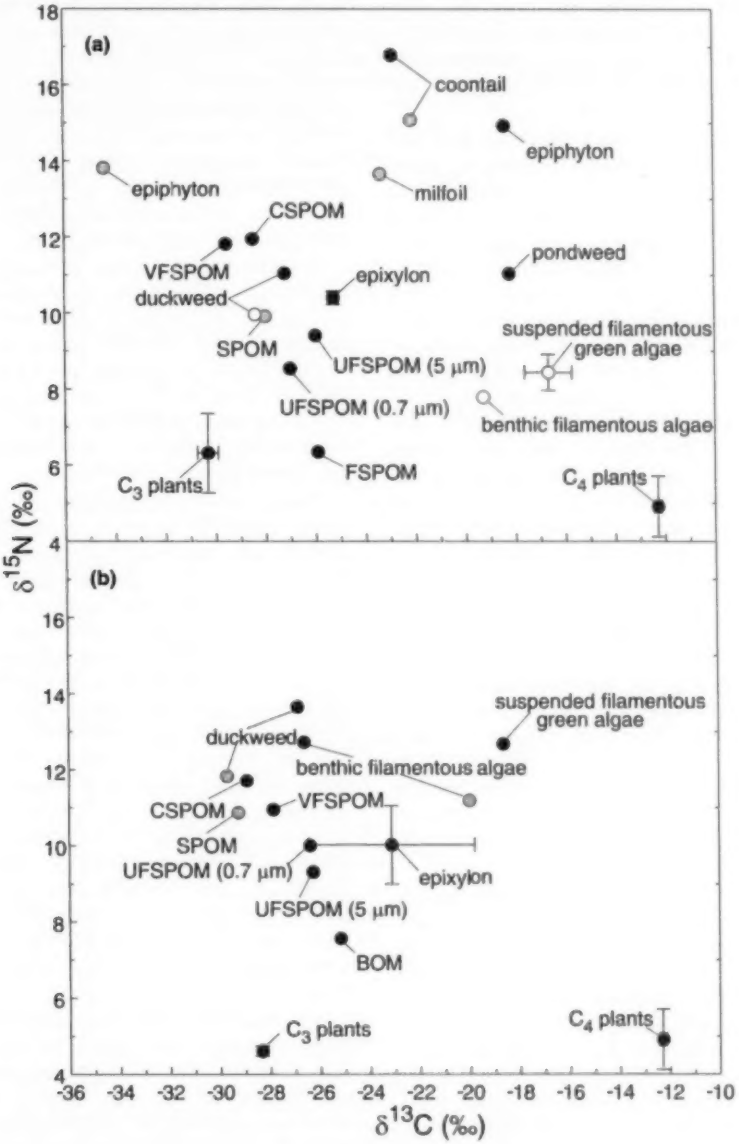
Fig. 1. Isotopic signatures of potential food sources ($\delta^{13}C$ and $\delta^{15}N$ compositions) at the study sites: (*a*) Savanna Bay and (*b*) Long Lake. Samples collected in fall 1998 are represented by shaded symbols; samples collected in spring 1999 are represented by open symbols; and samples collected in summer 1998 and 1999 are represented by solid symbols. Error bars represent the mean ± 1 standard error of 3–5 replicate samples. Potential food sources included C_3 and C_4 plants, various size fractions of suspended particulate organic matter (SPOM), benthic organic matter, and various types of filamentous and attached algae.



phytoplankton (SPOM, UFSPOM) signatures (Fig. 1*b*). There was also poor separation in the $\delta^{13}C$ signature of terrestrial C_3 plants, benthic filamentous and attached algae, and phytoplankton. In contrast, C_4 plants had unique $\delta^{13}C$ and $\delta^{15}N$ signatures well separated from other sources and would be readily identifiable if incorporated into consumer diets (Fig. 1*b*). Suspended filamentous green algae also had a unique signature in Long Lake; however, seasonal and between-sample variability was not assessed for this group (Fig. 1*b*).

Seasonal comparison of energy dependence and trophic structure

Potential carbon sources for consumers in Savanna Bay in fall included epiphyton, SPOM, and terrestrial C_3 plants (Fig. 2). There was no apparent dependence on C_4 plants or macrophytes by any consumers during any season (Fig. 2). Snails (Gastropoda) had variable $\delta^{13}C$ ratios (high standard errors) that likely reflected variability in $\delta^{13}C$ of algae. Damselfly (Zygoptera) and dragonfly (Anisoptera) larvae, both of which prey on macroinvertebrates, were not enriched

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in ^{15}N relative to primary consumers, whereas alderfly (Sialidae) larvae (also predators) were enriched over primary consumers. $\delta^{13}C$ and $\delta^{15}N$ measurements indicated that bluegill and gizzard shad appeared to derive carbon from benthic macroinvertebrates in fall and were enriched in $\delta^{15}N$ relative to primary and secondary invertebrate consumers (Fig. 2*b*). Bluegill had a mean $\delta^{15}N$ ratio 2‰ higher than gizzard shad, indicating that bluegill fed at a higher trophic level. Fish did not appear to feed on zooplankton during fall, given the high $\delta^{15}N$ values observed for copepods (Fig. 2*b*).

In spring, organic matter sources in Savanna Bay that could have supported consumers included terrestrial C_3 plants and duckweed (Fig. 2*c*). Phytoplankton and attached algae were not sampled, so we could not assess the importance of these sources. Suspended filamentous green algae, benthic filamentous algae, and C_4 terrestrial plants did not appear to have been important carbon sources for consumers at this time of the year. Zooplankton may have been an important food source for secondary consumers, based on combined $\delta^{13}C$ and $\delta^{15}N$ ratios; however, because these signatures fell within the range of several other macroinvertebrate consumers, it was difficult to assess their relative importance (Fig. 2*c*). Chironomids (Chironomidae) and oligochaetes (Oligochaeta) had highly variable $\delta^{13}C$ ratios, suggesting that these groups had broad diets consisting of many different sources. Bluegill and gizzard shad could have derived energy through either benthic or pelagic trophic pathways.

During spring, predatory macroinvertebrates, including larval damselflies, ceratopogonids (Ceratopogonidae), glass shrimps (Palaemonidae), and alderfly larvae (Sialidae) were enriched in ^{15}N relative to nonpredatory benthic invertebrates such as chironomids (Fig. 2*c*). However, glass shrimps had higher $\delta^{15}N$ ratios than bluegill and gizzard shad, suggesting they were not a significant prey resource for fish. Bluegill and gizzard shad were enriched in ^{15}N relative to both predatory and nonpredatory benthic invertebrates and zooplankton, with a $\delta^{15}N$ ratio intermediate to these prey groups, suggesting a mixed diet comprised of organisms from two or more of these groups.

Organic matter sources that could support consumers in Savanna Bay during summer included CSPOM (colonized C_3 litter), VFSPOM, UFSPOM, and epixylon (Fig. 2*d*). In contrast, fresh litter from C_3 plants, FSPOM, and C_4 plants did not appear to contribute significant energy to the food web. A large ^{15}N enrichment (+5.6‰) occurred after C_3 terrestrial plant litter was colonized by bacteria and other heterotrophs (CSPOM vs. C_3 plants). Epixylon did not appear to be an important carbon source for consumers, except possibly for amphipods (Amphipoda; Fig. 2*d*). In summer, consumer $\delta^{13}C$ ratios could be divided into two well-separated groups, one made up of mussels, chironomids, heptageniid mayflies (Heptageniidae), corixids, and zooplankton and the other group made up of amphipods, belostomatids (Belostomatidae), larval dragonflies, and notonectids (Notonectidae; Fig. 2*d*). This indicates that different carbon sources were important for consumers within each of these groups, likely resulting from differences in either microhabitat use or food preferences. Burrowing mayflies (Ephemeridae) had a consistent $\delta^{13}C$ ratio (mean and standard error) across all of the seasons, suggesting that their food sources may be less spatially and temporally dynamic. Alternatively, burrowing mayflies may either be limited to or selectively assimilating some specific component of total available carbon sources. Predatory macroinvertebrates were on average enriched in ^{15}N relative to nonpredatory benthic macroinvertebrates, but generally less than the predicted +3.4‰. Bluegill and freshwater drum appeared to derive biomass carbon primarily from macroinvertebrates. Both species were on average enriched in ^{15}N by 1.8‰ to 6.2‰ over invertebrate prey, indicating one or two trophic levels beyond primary consumers. Gizzard shad could have derived energy either directly from CSPOM or from any combination of CSPOM, benthic invertebrates, and copepods (Fig. 2*d*). Gizzard shad had $\delta^{15}N$ ratios approximately 2‰ lower than those of bluegill and freshwater drum, suggesting gizzard shad fed at a lower trophic level except during spring.

Overall, ^{13}C signatures of Long Lake consumers were much more depleted than in Savanna Bay (Figs. 2, 3). $\delta^{13}C$ ratios of many consumers were well separated from the terrestrial C_3 and C_4 plant signatures, which suggests that autochthonous production was an important food resource (Fig. 3). In all three seasons, detritus from C_3 plants could be an important source for several consumers, but dependence on C_4 plants was not indicated for any consumer for any season.

During fall, the food sources most closely allied with consumer signatures in spring were SPOM and duckweed, although we could not sample any other autochthonous components at this time of the year (Fig. 3*b*). *Daphnia* spp. and copepods were depleted in ^{13}C in both fall and spring relative to other consumers (Fig. 3*b*). It is possible that copepods and *Daphnia* assimilated the phytoplankton component of SPOM; however, SPOM was too enriched in ^{13}C to have been a direct food source (Fig. 3*b*). Heptageniid mayflies, amphipods, chironomids, larval damselflies, crayfish, and fish were enriched in ^{13}C relative to zooplankton. Other consumers were likely dependent on an alternative energy source, which could include either colonized C_3 plant litter or duckweed. Predatory macroinvertebrates, including *Chaoborus* spp. (zooplankton predators), glass shrimps, damselflies, and ceratopogonids, were, on average, enriched in ^{15}N over nonpredatory invertebrates. Bluegill and gizzard shad were also enriched relative to nonpredatory macroinvertebrates, with $\delta^{15}N$ ratios 2.2‰ to 4.9‰ higher than potential prey items.

We could not obtain any autochthonous carbon sources (algae) in Long Lake during spring; therefore, conclusions concerning the sources supporting consumers were limited for this season (Fig. 3*c*). *Daphnia*, copepods, and chironomids were considerably more depleted in ^{13}C than C_3 plants (Fig. 3*c*). A second group of consumers in the spring food web (snails, oligochaetes, Isopoda, Corixidae, and amphipods) was more enriched in ^{13}C than zooplankton and chironomids. Ceratopogonids and crayfish had $\delta^{13}C$ ratios intermediate to those of the first two groups of invertebrate consumers and a higher $\delta^{15}N$ ratio, consistent with their role as predators on benthic macroinvertebrates. Based on $\delta^{13}C$ ratios, bluegills appeared to derive their biomass carbon from benthic invertebrates rather than from zooplankton.

Snails feed on surfaces covered with algae, and summer $\delta^{13}C$ and $\delta^{15}N$ ratios for snails fell in the range of signatures observed for epixylon (Fig. 3*d*). Both *Daphnia* and benthic

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Fig. 2. $\delta^{13}C$ and $\delta^{15}N$ signatures of potential food sources and consumers for Savanna Bay in various seasons: (*a*) summer 1998, (*b*) fall 1998, (*c*) spring 1999, and (*d*) summer 1999. Open circles, potential food sources; shaded triangles, invertebrate consumers; solid squares, fish. Error bars represent the mean ± 1 standard error of 3–5 replicate samples. Abbreviations: zeb mus, zebra mussel; centr, centrarchid; cypr, cyprinid.

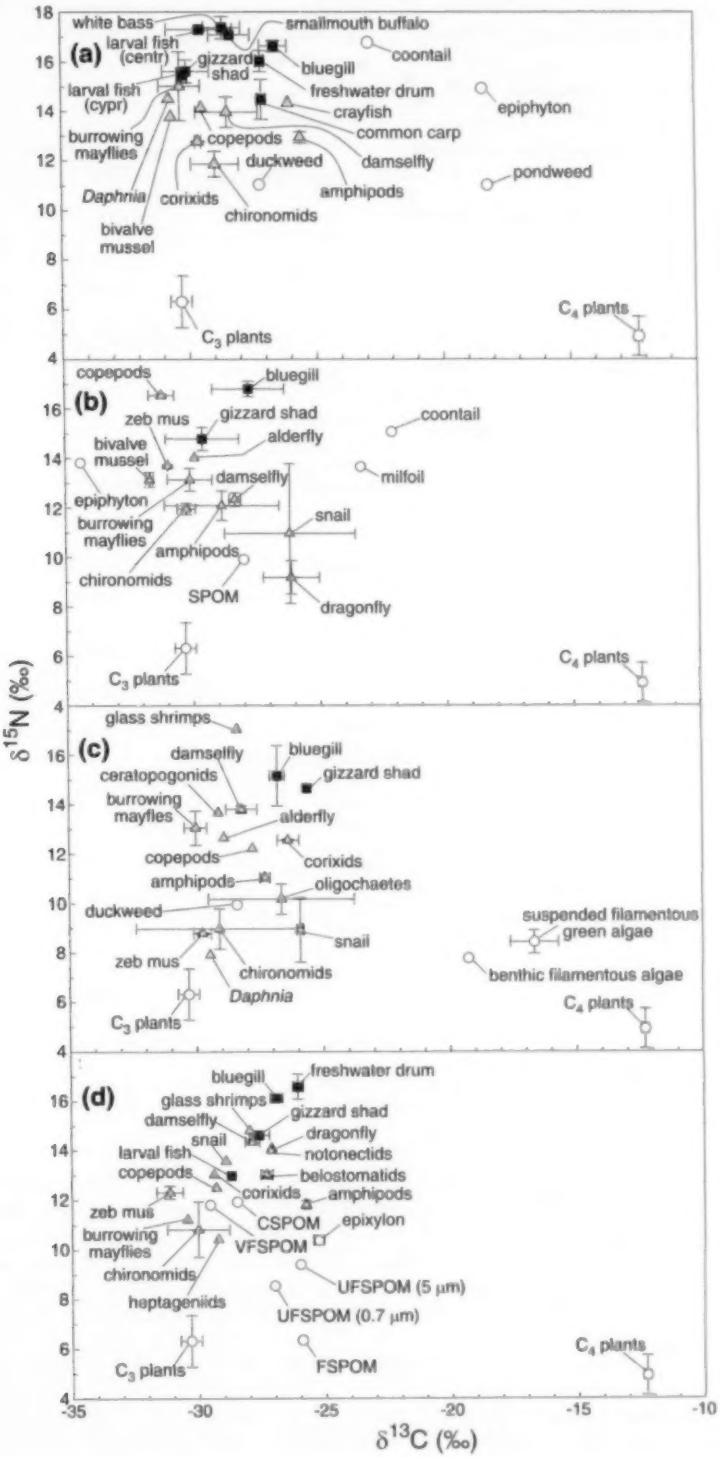

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Fig. 3. $\delta^{13}C$ and $\delta^{15}N$ signatures of potential food sources and consumers for Long Lake in various seasons: (*a*) summer 1998, (*b*) fall 1998, (*c*) spring 1999, and (*d*) summer 1999. Open circles, potential food sources; shaded triangles, invertebrate consumers; solid squares, fish. Error bars represent the mean ± 1 standard error of 3–5 replicate samples.

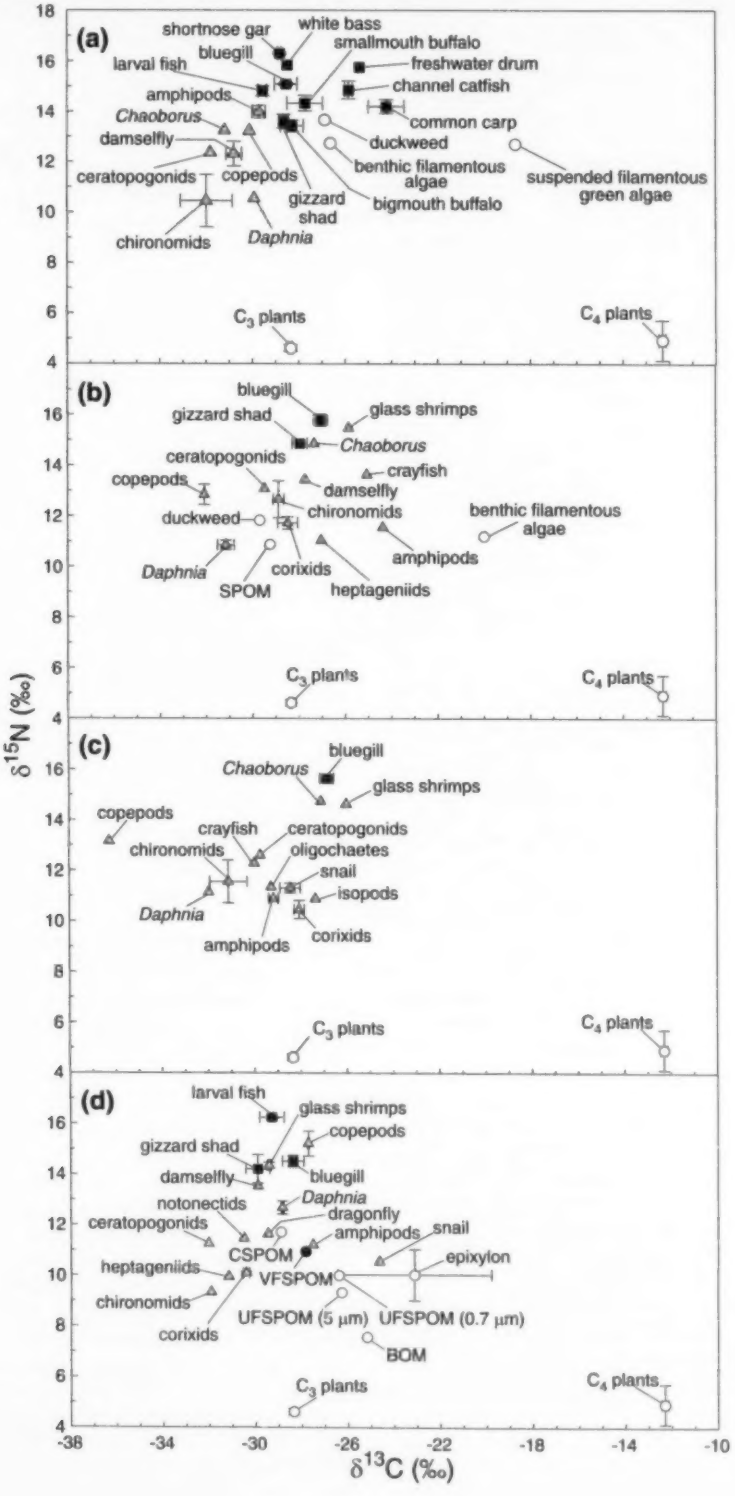

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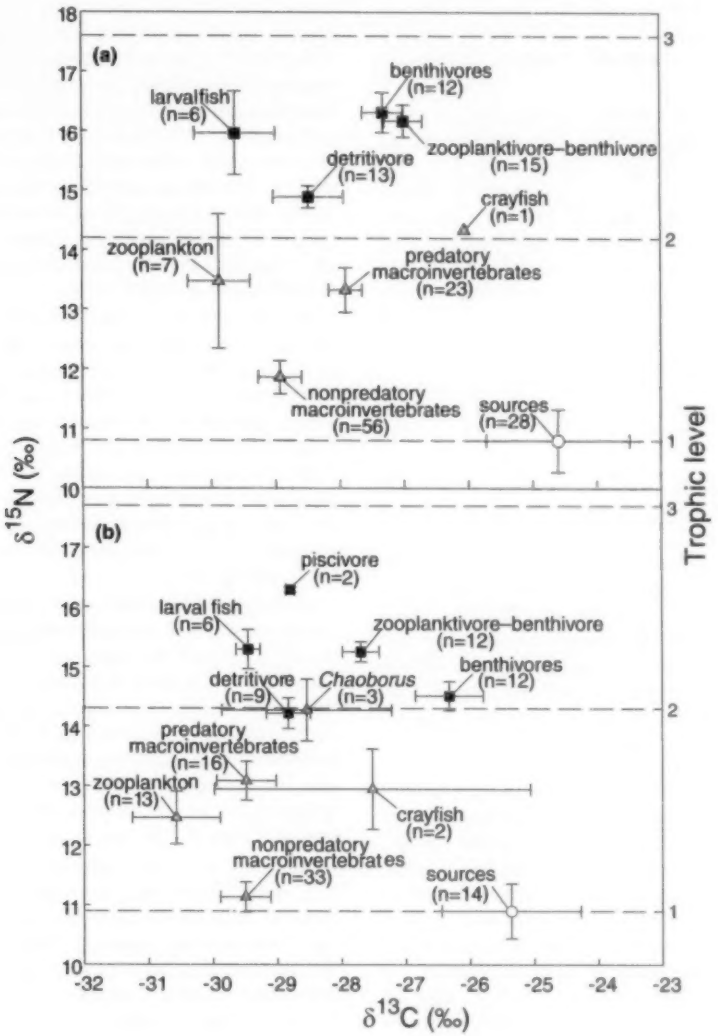
Fig. 4. $\delta^{15}N$ and $\delta^{13}C$ values of consumers partitioned into major feeding guilds at the study sites: (*a*) Savanna Bay and (*b*) Long Lake. Open circles, potential food sources; shaded triangles, invertebrate consumers; solid squares, fish. Data points represent the mean ± 1 standard error of all consumers from that feeding guild (or potential food sources) across all seasons combined. Feeding guilds include the following fish species (detritivore, gizzard shad; zooplanktivore–benthivore, bluegill; benthivores, freshwater drum, smallmouth buffalo, common carp, channel catfish, white bass; piscivore, shortnose gar). The total number of samples used in each calculation is listed in parentheses. Broken lines represent predicted trophic levels based on a trophic enrichment of 3.4‰ over the mean source $\delta^{15}N$.



invertebrates (e.g., dragonflies) had $\delta^{13}C$ and $\delta^{15}N$ values appropriate to have been food sources for bluegill (Fig. 3*d*). Bluegill and gizzard shad were enriched in ^{15}N by approximately 0.7‰ to 5.2‰ relative to most invertebrate consumers (Fig. 3*d*). However, copepods and glass shrimps had equal or higher $\delta^{15}N$ ratios. Predatory macroinvertebrates also had higher $\delta^{15}N$ ratios than their prey. For example, ceratopogonids had a $\delta^{15}N$ signature that was 1.9‰ higher than chironomids, an abundant prey item. Larval fish had $\delta^{15}N$ values similar to adult fish, which may reflect the carryover of parental nitrogen that occurs in larval fish.

Interannual variability in energy dependence and trophic structure

To assess between-year variability in stable isotope signatures, we compared resources and consumers at each backwater site in the summers of 1998 and 1999. In Savanna Bay, consumers generally had similar stable isotope signatures among years. With the exception of copepods and gizzard shad, all consumers sampled in both years had mean $\delta^{13}C$ and $\delta^{15}N$ ratios that were within ±1‰ between years (Figs. 2*a*, 2*d*). Gizzard shad were 2.5‰ more depleted in ^{13}C in 1998 than in 1999, indicating that either the signature

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of the sources assimilated by gizzard shad changed between years or that gizzard shad shifted their diet. Copepods were 1.7‰ more enriched in ^{15}N in 1998 than in 1999, likely reflecting a shift in the isotopic composition of phytoplankton. In Long Lake, chironomids, ceratopogonids, larval damselflies, gizzard shad, and bluegill differed, on average, by less than 1‰ for both $\delta^{13}C$ and $\delta^{15}N$ between years (Figs. 3*a*, 3*d*). Amphipods, copepods, and *Daphnia* differed appreciably between years, likely reflecting the spatially and temporally dynamic stable isotope signatures of their food source.

Trophic enrichment in $\delta^{15}N$ among feeding guilds

Nonpredatory macroinvertebrates in both sites were slightly enriched (≤1‰) over the average "source" signature, but much less than the expected 3.4‰ (Fig. 4). Similarly, predatory macroinvertebrates were enriched in ^{15}N over nonpredatory macroinvertebrates by only a maximum of 2‰. Piscivorous fish (shortnose gar) in Long Lake were also only enriched in ^{15}N relative to their prey (assumed to be gizzard shad) by 2.0‰; however, several other fish categories (benthivorous fish, bluegill, gizzard shad, and larval fish) exhibited enrichments close to the expected 3.4‰.

Discussion

Most stable isotope studies have not assessed spatial and temporal variation in source signatures or food web structure, although there are a few exceptions (Gu et al. 1994; Yoshioka et al. 1994). In addition, many stable isotope studies have examined only one autochthonous food source during one season (often epilithon in rivers or SPOM in lakes) and then have used it to represent all autochthonous carbon in the system (see review by del Giorgio and France 1996). Autochthonous source signatures in our backwater lakes were highly variable between sites and among seasons. Aquatic primary producers, including attached algae and phytoplankton, also overlapped the range of $\delta^{13}C$ observed for terrestrial C_3 plants. Lack of separation among sources limited our ability to distinguish among organic matter sources that support consumers. Macrophytes and C_4 terrestrial plants, however, had unique signatures well separated from other sources. Dependence on macrophytes (except duckweed) and C_4 plants was not indicated for any consumer in any season. Epixylon, benthic filamentous algae, and suspended filamentous green algae also appeared to be of limited importance as energy sources for consumers in food webs of backwater lakes, except in summer when epixylon may have some importance. All consumers fell in the range of $\delta^{13}C$ and $\delta^{15}N$ values observed for algae and decomposing terrestrial C_3 vegetation (CSPOM) from the riparian zone. Our data support several recent stable isotope studies that have also shown macrophytes to contribute little direct carbon to aquatic food webs despite their abundance (Bunn and Boon 1993; Keough et al. 1996). Macrophytes, however, may enter the food web as detritus, undergoing complex chemical and isotopic fractionations as microbes assimilate them. Such changes may make it difficult to detect macrophytes as indirect sources (Keough et al. 1996).

In lakes, phytoplankton is typically considered the most important carbon source supporting secondary consumers and fish growth (Gu et al. 1994, 1996; Yoshioka et al. 1994). Recently, however, there has been increased evidence for benthic producers as energy sources in lakes. For example, a meta-analysis of stable isotope studies performed in lakes revealed a nearly equal dependence of aquatic consumers on benthic algae and phytoplankton (Hecky and Hesslein 1995). Terrestrial detritus can also be an important energy source for aquatic organisms in small, oligotrophic lakes (France 1997). Our data indicate that for backwater lakes, either phytoplankton or detritus from C_3 plants are important in supplying carbon to invertebrate and fish consumers. Epixylon and benthic filamentous algae appeared to be important sources for consumers such as amphipods and snails in some seasons, but not in others. Probably some combination of allochthonous and autochthonous sources is important to backwater consumers, but the relative contribution of each could not be assessed because of the lack of separation and high within-source variability observed among SPOM, CSPOM, and attached algae.

Recent isotopic evidence suggests that benthic algae and terrestrial riparian vegetation can play important roles in supporting invertebrate consumers and fish in lakes (Hecky and Hesslein 1995; France and Steedman 1996; France 1997), and our results indicate similar relationships for backwater lakes of large rivers. We found little evidence that higher consumers (primarily fish) assimilated much zooplankton; instead they seemed to have fed primarily on benthic macroinvertebrates, which can consume a broad range of both detrital and autochthonous sources (reviewed in Cummins 1973).

Omnivory is common in freshwater food webs, especially among freshwater fish assemblages (Vadas 1990). Our data strongly support this observation in backwater ecosystems. Fish $\delta^{13}C$ signatures were typically intermediate among several different prey $\delta^{13}C$ signatures and had intermediate $\delta^{15}N$ values relative to predatory and nonpredatory benthic macroinvertebrates. Some macroinvertebrate consumers also appear to include a wide range of items in their diet, as indicated by the variability in their $\delta^{13}C$ and $\delta^{15}N$, suggesting that omnivory is important for these consumers as well.

High levels of interannual variability were observed in $\delta^{13}C$ and $\delta^{15}N$ for algal sources (all sites) and for some consumers. Amphipods (Savanna Bay) and zooplankton (both sites) had variable signatures between years, likely reflecting the dynamic signatures of their food source. Signatures of all other invertebrate consumers were within ±1‰ between years for both $\delta^{13}C$ and $\delta^{15}N$, suggesting that predictable patterns of energy dependence and trophic structure occur between years. Except for gizzard shad in Savanna Bay, fish had consistent isotopic ratios across seasons within and between years likely because fish tissues are time-integrated over months to years (Hesslein et al. 1993).

We observed trophic enrichments for $\delta^{15}N$ that were considerably lower than the average 3.4‰ increase predicted from a synthesis of previous stable isotope studies. Lower than expected trophic enrichments were found for (1) predatory macroinvertebrates in Savanna Bay (1.4‰), (2) shortnose gar (2.3‰) in Long Lake, and (3) benthivorous fish (0.3–6.2‰) in both backwaters. Results from other isotope studies have demonstrated that trophic enrichments for $\delta^{15}N$

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can vary depending on the trophic level, animal-diet system, or ecosystem under consideration, and lower than expected (i.e., <3.4‰) enrichments often occur (Pinnegar et al. 2001; Vander Zanden and Rasmussen 2001; Zah et al. 2001). For example, parasites were not enriched in $\delta^{15}N$ with respect to their fish hosts, and endoparasites were actually depleted relative to fish host tissues (Pinnegar et al. 2001). Minagawa and Wada (1984) reported a wide range in $\delta^{15}N$ trophic enrichment values across taxa (0–9‰) and suggested that such variation could be due to either incomplete knowledge of food sources used or dynamic biochemical and environmental conditions encountered by the organism. The results of these studies and ours indicate that care should be taken when assessing specific trophic relationships in the absence of good diet information and when physiological processes that fractionate isotopes are unknown (Gannes et al. 1997). Despite the highly variable relationship between $\delta^{15}N_{animal}$ and $\delta^{15}N_{diet}$, there is strong evidence that a repeatable pattern of $\delta^{15}N$ trophic enrichment exists for lakes, although the relationship was shown to differ between herbivores (mean = 2.5‰) and carnivores (mean = 3.4‰) (Vander Zanden and Rasmussen 2001). Data from the present study, combined with the relationships observed for lakes (Vander Zanden and Rasmussen 2001) and streams (Zah et al. 2001), suggest that trophic enrichment patterns are ecosystem-dependent and that unique enrichment factors must be developed for each ecosystem.

Backwater lakes differ from other lakes in that zooplankton do not appear to be strongly coupled to higher trophic levels, as typically assumed in the trophic cascade model of lake food webs (Carpenter and Kitchell 1988). This occurred despite the fact that zooplankton densities in backwater lakes are similar to those found in other lakes (Goodrich 1999). Adult fish instead appeared to derive energy from a mix of predatory and nonpredatory macroinvertebrates, suggesting that organic matter from benthic habitats may ultimately be the base of the food web fueling higher trophic levels in backwater lakes.

Stable isotope analysis is an important tool that can be used to understand feeding ecology, food web structure, and ecosystem level processes, but the method is a useful complement to controlled field–laboratory experiments or traditional gut content analyses rather than a substitute (Rounick and Winterbourn 1986). Stable carbon and nitrogen isotope analysis requires the presence of large and consistent separations in source signatures that can be tracked through consumers at higher trophic levels (Peterson and Fry 1987; Rounick and Winterbourn 1986). When there is high within-compartment (source) variability, multiple sources, and sources with overlapping signatures, the success of the stable isotope approach becomes increasingly limited. Despite these challenges, data from this study provided insight into the structural and functional aspects of food webs in backwater riverine habitats. Our isotopic data challenge the conventional wisdom that macrophytes are an important food source for aquatic consumers in shallow lakes and the view that food webs in lakes are primarily supplied with carbon fixed by phytoplankton. Instead, carbon from benthic and terrestrial habitats appear to be most important in supporting consumers in backwater habitats of large floodplain rivers.

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An estimate of chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat and redd capacity upstream of a migration barrier in the upper Columbia River

Timothy P. Hanrahan, Dennis D. Dauble, and David R. Geist

Abstract: Chief Joseph Dam on the Columbia River is the upstream terminus for anadromous fish because of its lack of fish passage facilities. Management agencies are currently evaluating the feasibility of reintroducing anadromous fish upriver of Chief Joseph Dam. We evaluated the physical characteristics of potential fall chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat in the upper section of Chief Joseph Reservoir. The objectives were to estimate the location and quantity of potential spawning habitat and to determine the redd capacity of the area based on spawning habitat characteristics. The suitability of the study area was estimated through the use of geomorphic analysis, empirical physical data, and modeled hydraulic data. We estimated that 5% (48.7 ha) of the study area contains potentially suitable fall chinook salmon spawning habitat. Potential spawning habitat is primarily limited by deep water and low water velocities, resulting in 20% (9.6 ha) of the potential spawning habitat being characterized as high quality. Estimates of redd capacity within potential spawning habitat range from 207 to 1599 redds. The results of our study provide fisheries managers with useful information for evaluating the complex issue of reintroducing anadromous fish to the Columbia River upstream of Chief Joseph Dam.

Résumé : Le barrage Chief Joseph sur le Columbia, qui ne possède pas de passe migratoire pour les poissons, est le point ultime de la remontée des poissons anadromes. Les agences de gestion étudient présentement la faisabilité d'introduire à nouveau des poissons anadromes en amont du barrage Chief Joseph. Nous avons évalué les caractéristiques physiques des habitats de fraye potentiels pour le saumon quinnat (*Oncorhynchus tshawytscha*) d'automne dans le secteur supérieur du réservoir Chief Joseph. Nos objectifs étaient d'estimer la répartition et la qualité de l'habitat potentiel de fraye et de déterminer le nombre possible de nids dans la région d'après les caractéristiques de l'habitat des frayères. Afin d'estimer l'utilisation potentielle de la région d'étude, nous avons fait une analyse géomorphologique, utilisé des données physiques empiriques et construit des modèles hydrauliques. Nous estimons que 5 % (48,7 ha) de la région d'étude contient des habitats de fraye potentiellement utilisables par le saumon quinnat d'automne. L'habitat potentiel de fraye est limité surtout par des eaux profondes et des courants lents; il n'y a donc que 20 % (9,6 ha) de l'habitat de fraye potentiel qui soit de bonne qualité. Notre estimation du nombre possible de nids dans l'habitat de fraye potentiel est de 207–1599 nids. Nos résultats fournissent aux gestionnaire de la pêche des informations utiles pour évaluer le problème complexe de la réintroduction de poissons anadromes dans le Columbia en amont du barrage Chief Joseph.

[Traduit par la Rédaction]

Introduction

Ocean-type (summer/fall) chinook salmon (*Oncorhynchus tshawytscha*) historically spawned in the mainstem of the upper Columbia River as far upstream as British Columbia, Canada, with a large number spawning near Kettle Falls, Washington, U.S.A. (river kilometre (rkm) 1124; Chapman 1943). Access to the upper river was blocked in the mid-20th century by the construction of hydroelectric dams lacking fish passage facilities. Grand Coulee Dam (rkm 957) was completed in 1941 and was the upstream terminus for chinook salmon until the completion of Chief Joseph Dam (rkm 874) in 1955, which is now the upstream migration barrier. Collectively, these two hydroelectric projects blocked access to 250 rkm of the historic spawning range of fall chinook salmon, accounting for approximately 25% of their total historic spawning range within the mainstem Columbia River. Of the seven species of Pacific salmon (*Oncorhynchus* spp.) historically found in the Columbia River Basin, fall chinook salmon were especially affected by hydroelectric development on the mainstem Columbia River because most populations carry out their entire freshwater life cycle within the

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mainstem habitats. Thus, they are particularly vulnerable to physical habitat modifications resulting from construction and operation of mainstem hydroelectric dams (Connor et al. 2002; Dauble et al. 2003).

There is now considerable debate within the Columbia Basin regarding management activities directed towards enhancement and restoration of mainstem habitat and anadromous salmonid populations. Much of the debate is centered on physical and operational modifications to hydroelectric dams and the related uncertainties regarding potential restoration sites and specific benefits to salmon (National Marine Fisheries Service (NMFS) 2000). Because most of the Columbia and Snake rivers are impounded, the only opportunities for increasing mainstem production of fall chinook salmon is by increasing the amount of riverine habitat available for spawning and rearing via operational changes of selected hydroelectric projects or by eliminating migration barriers to historic habitat. Management agencies are currently evaluating the feasibility of reintroducing anadromous fishes (including fall chinook salmon) upriver of Chief Joseph Dam. The evaluation includes determining the existing habitat conditions within the historic distribution areas and identifying factors that would potentially limit anadromous fish production, assuming fish passage issues could be resolved (U.S. Army Corps of Engineers (USACE) 2000).

Although Chief Joseph Dam creates a reservoir of significant size, the upper end of the reservoir contains segments with unconsolidated sediments, bars and islands, and riverine hydraulic characteristics, the extent of which depends on the flow regime from Grand Coulee Dam. In combination, all of these geomorphic characteristics define the river reaches toward which spawning fall chinook salmon have an affinity (Geist and Dauble 1998; Dauble and Geist 2000). Reconnaissance surveys suggested that the microhabitat in some portions of these segments exhibit the substrate composition, water velocity, and channel depth within the range that fall chinook salmon spawn in other segments of the Columbia River. However, no studies have quantitatively estimated the extent and location of potentially suitable spawning habitat based on physical characteristics. The objectives were (1) to estimate the location and quantity of potential spawning habitat, (2) to determine the redd capacity of the area based on spawning habitat characteristics, and (3) to identify physical habitat factors potentially limiting suitable spawning habitat upstream of Chief Joseph Dam.

Methods

Study area

Chief Joseph Dam creates a reservoir (Lake Rufus Woods) extending approximately 83 km upriver along the Columbia River, terminating at Grand Coulee Dam. At the watershed scale (10^3 km^2), the present landforms in the study area were shaped by glacial and flood processes and events during the Pleistocene epoch (Quigley and Arbelbide 1997). The resulting geology is a complex mix of basalt and granite bedrock mixed with alluvial and lacustrine deposits ranging from fine sand to large boulders.

The reservoir is largely a lake environment, with a short segment in the upper end of the reservoir exhibiting riverine characteristics under certain flow regimes. The riverine segment comprises the study area, extending from the tailwater of Grand Coulee Dam (rkm 956) downriver to approximately rkm 928 near Coyote Creek (Fig. 1). The upper section of the study area (rkm 947 – rkm 956) is largely stabilized by boulder riprap along the entire right bank (facing downstream) and extending into the majority of the channel. Several sections of the study area contain remnant alluvial deposits (point bars and lateral bars) created by the Columbia River pre-dam, which are now partially or entirely submerged. The two largest of these sections are Buckley Bar (rkm 942.5 – rkm 944.5) and Nespelem Bar (rkm 932 – rkm 934).

The physical and hydraulic characteristics of the study area are controlled by the discharge from Grand Coulee Dam, the corresponding tailrace water surface elevation, and the forebay elevation of Chief Joseph Dam. The daily discharge from Grand Coulee Dam during October and November has large amplitude, often ranging from 566 to 4245 $m^3 \cdot s^{-1}$ during a 24-h period.

Current physical channel characteristics

The physical channel characteristics of the study area were evaluated through a combination of empirical and modeled data. Historical hydrology data were used to determine the typical flow regime during October and November (fall chinook spawning period) in the study area. Hourly discharge records from Grand Coulee Dam were compiled for the months of October and November from the years 1967–1998. The 10, 50, and 90% exceedence discharges (Q_{10} = 3438.5 $m^3 \cdot s^{-1}$, Q_{50} = 2272.5 $m^3 \cdot s^{-1}$, Q_{90} = 1202.8 $m^3 \cdot s^{-1}$, respectively) from this flow record were used as inputs to the hydraulic modeling. The exceedence discharge indicates the discharge that is equaled or exceeded x% of the time.

Characterization of channel morphology and hydraulic modeling required a three-dimensional surface of channel-bed elevations (bathymetry) for the entire study area (28 rkm). Depth data were collected using a 200-kHz single-beam echosounder deployed from a boat. The data were collected along transects spaced 20–300 m apart (depending on channel complexity) oriented perpendicular to flow and along longitudinal transects oriented parallel to flow. The echosounder was operated to collect data at 3-s and 10-s intervals and was linked to a real-time differentially corrected global positioning system (DGPS) to provide submeter positional data. Both the depth and positional data were recorded to a database stored on a laptop computer for postprocessing. The water surface elevations during the bathymetry survey periods were recorded using four water level loggers set to record data at 15-min intervals. The level loggers were placed inside perforated standpipes and spaced throughout the study area. The elevations (North American Vertical Datum of 1988 (NAVD88)) of the standpipes were determined to within ±10.0 cm by completing a GPS survey using nearby control benchmarks of the National Geodetic Survey. Depth data from the bathymetry surveys were subtracted from corresponding water surface elevations, resulting in a comprehensive coverage of bathymetry point elevations. Nearshore topography data from U.S. Geological Survey (USGS) 7.5′ quadrangle maps were combined with the bathymetry points into a geographic information system (GIS) database to create a triangulated irregular network (TIN) model representing the

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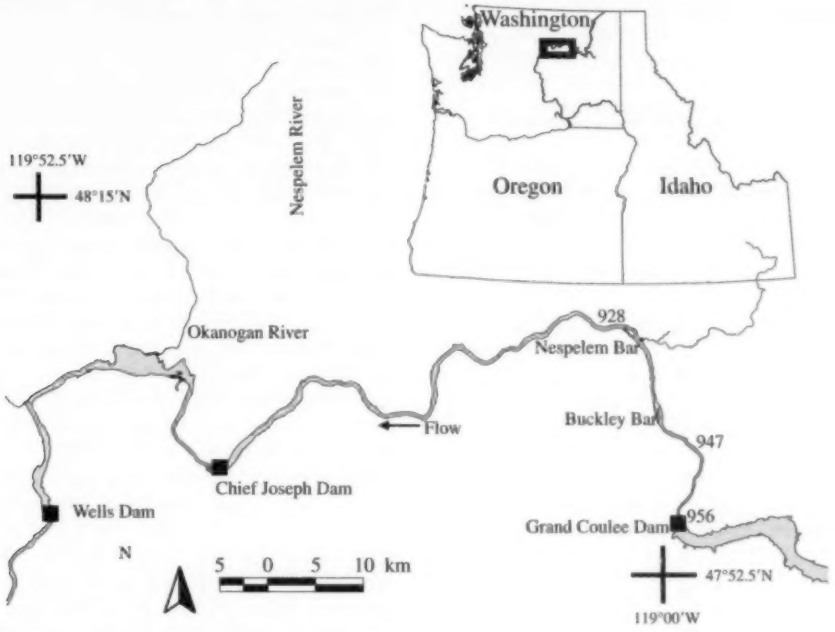
Fig. 1. The study area was located on the upper Columbia River, Washington, U.S.A., in the reservoir upstream of Chief Joseph Dam. The upper section of the reservoir contains riverine hydraulic characteristics extending from Grand Coulee Dam (river kilometre (rkm) 956) downstream to near the Nespelem River confluence (rkm 930).



interpolated bathymetry surface for the study area. The TIN model was converted to a raster GIS datafile (ArcInfo Grid) with a 3-m cell resolution in order to estimate channel-bed slope. The slope of each 3 m × 3 m cell was calculated in the GIS using an algorithm that fits a plane to the elevation values of a 3 cell × 3 cell neighborhood around the cell being processed. The slope for a given cell is calculated using the average maximum technique based on the surrounding 3 cell × 3 cell neighborhood (Burrough 1986).

Substrate data were collected by underwater videography in February 2001, using a video-based adaptation of the pebble count method. The video system consisted of a high-resolution monochrome camera with wide-angle lens connected to an 8-mm camera recorder located on the boat. The camera was placed inside a waterproof housing and mounted on a weighted platform containing two downward-pointing lasers, providing reference scale within each video image. Positional data were recorded with a real-time DGPS.

The pebble count method typically dictates sampling 100 stones selected without bias from specific geomorphic features (Wolman 1954; Church et al. 1987; Kondolf 2000). The study area was delineated into nine distinct geomorphic units, based on pre-dam channel morphology, present morphology, and hydraulic characteristics. Within each unit, samples were collected in a spatially distributed manner to ensure uniform coverage of each unit (Wolcott and Church 1991; Crowder and Diplas 1997). This sampling scheme is appropriate for obtaining overall sediment size characteristics of a distinct geomorphic unit, or even for an entire reach (Wolcott and Church 1991; Crowder and Diplas 1997). A minimum of 100 substrate images was collected by underwater videography within each geomorphic unit. Equipment restrictions limited substrate surveys to areas with water depths ≤12.2 m, which is greater than the maximum documented fall chinook spawning depth of 9.1 m (summarized in Geist and Dauble 1998).

The individual substrate images were processed with image analysis software. Substrate images were treated as pebble counts in that the processing software automatically selects the grain at the center of each image. The grain was first digitized by the computer operator and then measured by the software to provide an estimate of the length of the apparent long (*a*) and intermediate (*b*) axes for each grain.

The grain size estimates were used to develop cumulative grain size distributions for each geomorphic unit. In addition to total grain size distributions (e.g., where d_{84} represents the grain size in mm and 84% of the sampled grains were finer than this size), the geometric mean (d_g), geometric sorting coefficient (s_g), and geometric skewness coefficient (sk) were also calculated for each geomorphic unit (Kondolf and Wolman 1993; Kondolf 2000).

Substrate summary statistics and indices were incorporated into the GIS database for mapping and habitat modeling. The d_g, sk, and total distribution of each substrate sampling unit were used to categorize it as "suitable" or "not suitable". A unit was categorized as "suitable" if (*i*) the d_g, d_{84}, and d_{75} values (i.e., grain size in mm) were within the criteria defining the size range of suitable fall chinook spawning substrate (Table 1) and (*ii*) the unit lacked an appreciable amount of fine sediment as indicated by strongly negatively skewed (i.e., sk value) grain-size distributions (Kondolf and Wolman 1993; Kondolf 2000).

Estimates of depth and velocity were derived from the results of hydraulic modeling based on the River2D model (Ghanem et al. 1996; Waddle et al. 2000). River2D is a two-dimensional, depth-averaged finite element model that

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Table 1. Criteria defining suitable fall chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat.

Variable	Values
Depth	0.30–9.50 m
Velocity	0.25–2.25 m·s^{-1}
Substrate	25–305 mm
Channel-bed slope	0.0–5.0%

calculates hydraulic parameters based on the principles of conservation of mass and momentum. The model requires inputs for channel-bed elevations, channel-bed roughness information, and stage–discharge relationships at the model boundaries.

The computational mesh for the hydraulic model of the study area was constructed from the TIN bathymetry surface and resulted in a node spacing of approximately 20 m in both the x and y directions. At each node of the mesh, the channel-bed elevation and roughness height were specified based on the bathymetry and substrate data. The model was run for the 10, 50, and 90% exceedence discharges (Q_{10}, Q_{50}, Q_{90}) described above. Corresponding stage data for the upstream and downstream model boundaries were provided by the U.S. Army Corps of Engineers Seattle District (Ron Malmgren, Hydraulics and Hydrology Section, U.S. Army Corps of Engineers, P.O. Box 3755, Seattle, WA 98124-3755, personal communication), based on the results of their one-dimensional unsteady hydraulic model (UNET). The stage at the downstream boundary (rkm 928) corresponded to the forebay elevation (291 m above the 1929 National Geodetic Vertical Datum) at Chief Joseph Dam that is typical during the October–November time period. The model node locations and roughness height were adjusted until the results from preliminary model runs were validated to be within acceptable variation from empirical stage and velocity data. For the Q_{50} discharge, modeled water surface elevations (WSE) were within 9 cm of the WSE recorded on the level loggers. Regressions of modeled versus empirical depth-averaged velocity yielded a coefficient of determination $r^2 = 0.70$ with a standard error of 0.10 cm·s^{-1}. Once the bathymetry, bed roughness, and stage–discharge data were prepared, the model was run for each discharge scenario until mass balance convergence was achieved. The model was considered converged when the difference between the inflow and outflow rate was less than 1% of the input discharge (Waddle et al. 2000).

The results from each model run were output to ASCII text files and imported into the GIS database, providing hydraulic data (e.g., depth and velocity) for each node in the study area. A continuous surface of each hydraulic variable was created using an inverse distance weighting interpolation. The interpolated value of each cell on the surface was determined by a linearly weighted average of the cell's three nearest nodes. The weight was a function of inverse distance such that nearby sampling points had more influence on the interpolated value. The resulting surfaces for depth and velocity had cell sizes of 9 m^2 (3 m × 3 m) and were used to estimate potential spawning habitat. A cell size of 3 m was chosen to estimate hydraulic conditions at a fine-scale relative to channel size (mean widths ~300–800 m), particularly near the shorelines.

Potential spawning habitat

Geomorphic analysis at the river segment scale (1–5 channel widths in length) was completed to identify areas with the highest potential for spawning. The analysis was based on interpretation of bathymetry, channel planform, substrate types, and geologic features of the shoreline. Cross-sectional and longitudinal plots of hydraulic geometry were used to identify segments with asymmetrical bedform (as opposed to trapezoidal, uniform cross section). Those segments of the study area exhibiting depositional features (unconsolidated alluvium, lateral bars, islands, midchannel bars) and asymmetrical cross sections were considered to have greater potential as a spawning area than segments without these characteristics. All segments were mapped in the GIS, coded as "potential habitat" or "not suitable", and included in the spawning habitat modeling. Criteria for coding segments as geomorphically suitable or not suitable were the same as those used by Dauble et al. (2003).

Estimates of potential spawning habitat were completed using a two-staged approach. The first stage categorized each 3 m × 3 m cell of the river as either suitable or not suitable for fall chinook salmon spawning habitat. This binary method identified the location and quantity of potential spawning habitat by comparing physical habitat characteristics against suitability criteria for fall chinook salmon spawning habitat. Our second stage of the approach assigned habitat suitability index values (weights) to each cell of suitable spawning habitat estimated from the binary modeling, thereby partitioning the suitable habitat into categories ranging from low to high quality. Both stages of the approach, binary and suitability index, result in the same total amount of potential spawning habitat.

The first step of the binary habitat modeling was to incorporate the results of the geomorphic analysis. This limited the subsequent habitat modeling to those areas considered geomorphically suitable as fall chinook salmon spawning habitat. Next, we estimated the location and quantity of potential spawning habitat by comparing physical habitat characteristics against suitability criteria for fall chinook salmon spawning habitat. The range of values describing suitable spawning habitat criteria was compiled from other fall chinook salmon spawning habitat studies in the mainstem Columbia and Snake rivers (Table 1; Geist and Dauble 1998; Groves and Chandler 1999; Geist et al. 2000). Physical habitat characteristics were estimated for all flow scenarios and included the variables depth, velocity (depth-averaged at each 9-m^2 cell), substrate, and channel-bed slope for the entire study area.

Binary habitat modeling provides estimates of the quantity and location of suitable habitat but does not result in any indication of a suitable area's value relative to some optimal value. To account for this, we developed suitability index (SI) curves for depth and velocity and used those curves to model the composite SI for the study area. We focused on depth and velocity because initial empirical data suggested that these physical characteristics might limit suitable spawning habitat, largely as a result of the study area's loca-

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tion in a transition area between the riverine environment of the Grand Coulee Dam tailrace and the backwater influence from Chief Joseph Dam.

We developed our depth and velocity SI curves based on data from the Hanford Reach of the Columbia River (D. Geist, unpublished data). The Pacific Northwest National Laboratory (PNNL) collected depth and velocity data from over 220 redds among nine different spawning areas, representing a variety of physical settings. All of the data were normalized to a constant discharge to account for the large fluctuating flows within the study area. We completed a frequency analysis with the depth and velocity data, resulting in probability-of-use values (SI curves) for a range of hydraulic conditions (Bovee and Cochnauer 1977; Bovee 1995). The SI curves represent weighted criteria, where a value of 1.0 indicates the optimum condition for a given hydraulic variable. Because our data sets did not contain frequency of occurrence data for the complete range of values for observed fall chinook salmon spawning (i.e., Table 1), the SI curves were adjusted at the lower and upper ends to include values reported in other fall chinook salmon spawning habitat studies in the Columbia and Snake rivers (Chapman et al. 1986; Swan 1989; Groves and Chandler 1999). The SI curves were adjusted through range and optimum analysis (Bovee and Cochnauer 1977); however, the additional depth and velocity values were always assigned an SI value ≤ the nearest value from the original SI curve.

The habitat suitability modeling proceeded by assigning SI values to the depth and velocity grids for each discharge scenario. As with the binary habitat modeling, the suitability modeling was limited to those areas considered geomorphically suitable as fall chinook spawning habitat. To include the entire suitable habitat estimated with the binary model, the variables of substrate and slope were assigned SI values of either 1.0 or 0.0 based on the values in Table 1 and included in the calculation of the composite SI (CI) for the study area. The CI was calculated as the geometric mean of the input variables:

$$(1) \qquad CI = (SI_1 \times SI_2 \times \ldots \times SI_n)^{1/n}$$

where SI_n is the suitability index value for variable n, and n is the number of input variables. Calculating the CI based on geometric mean allows for compensatory relationships among variables, but not as much as the arithmetic mean (U.S. Fish and Wildlife Service (USFWS) 1981). For example, if one variable's SI value is 0.0, the geometric mean will calculate the CI to zero also, meaning that if one variable is outside the range of suitable criteria, then the other variables cannot compensate for it. The resulting CI for each discharge scenario represents the weighted suitability of the study area, where a value of 1.0 indicates optimum potential fall chinook salmon spawning habitat.

Redd capacity

Estimates of production potential were based on the potential redd capacity provided by the area estimated to be suitable spawning habitat. Observations from studies in the Columbia River indicate that spawning fall chinook salmon utilize a relatively small proportion of seemingly suitable habitat within a contiguous area (Dauble and Watson 1997; Geist and Dauble 1998; Geist et al. 2000). The amount of potentially suitable habitat predicted with the binary and suitability index models described above was adjusted by a range of percentages, providing lower and upper estimates of reduced suitable area based on proportional utilization. Specifically, the reduced suitable area was calculated as 5–30% (in increments of 5%) of the original potential suitable area, reflecting the range of proportional use (Geist et al. 1997; Swan 1989; Visser 2000).

Redd capacity was defined as the total number of redds required to fill a given area of suitable spawning habitat. Two different methods were used to estimate redd capacity. The first method used the average size of a fall chinook salmon redd divided into the amount of suitable spawning habitat. Average redd sizes were from the Hanford Reach of the Columbia River and included 17 m^2 (n = 262; Chapman et al. 1986), 21 m^2 (n = 1500; 1994 data in Visser 2000), and 23 m^2 (n = 1500; 1995 data in Visser 2000). This method of calculating redd capacity results in estimates at the upper end of the range, as it does not account for inter-redd spacing.

The second method for estimating redd capacity was based on the average area used by a redd, including inter-redd spacing, divided into the amount of suitable spawning habitat. Values for inter-redd spacing were taken from studies in the Hanford Reach and include 3.4 m (Geist et al. 1997) and 2.8 m (Visser 2000). These values were applied to the average redd sizes, resulting in average area used ranging from 83 to 117 m^2.

Both methods of estimating redd capacity were applied to all discharge scenarios. The total redd capacity estimated for the study area was calculated based on the reduced suitable spawning area (calculated as 5–30%, in increments of 5%, of the original potential suitable area), reflecting a range of proportional use.

Results

Potential spawning habitat

Based on the binary habitat modeling, the estimate of total potential fall chinook salmon spawning habitat in the study area (rkm 928 – rkm 956) ranged from 33 ha to 50 ha, depending on the discharge regime from Grand Coulee Dam. The discharge representing the median hourly flow during the fall chinook salmon spawning period (i.e., the Q_{50} flow) resulted in a potential spawning habitat estimate of 48.7 ha, or 5.0% of the total study area (Table 2). The potential spawning habitat was concentrated in two general areas, Buckley Bar and Nespelem Bar, with smaller patches occurring just upstream of both of those areas (Fig. 2). The potential spawning habitat at Buckley and Nespelem bars represented 32% (15.6 ha) and 44% (21.5 ha) of the total potential spawning habitat, respectively. In addition to being located in areas of suitable depth, velocity, substrate, and bed slope, the potential spawning areas were also spatially correlated to channel bars formed by the pre-dam river (Fig. 3).

Within the potential spawning habitat areas, water depths toward the deeper end of the suitable range and water velocities toward the slower end of the suitable range dominated the available habitat (Fig. 4). For example, under the Q_{50}

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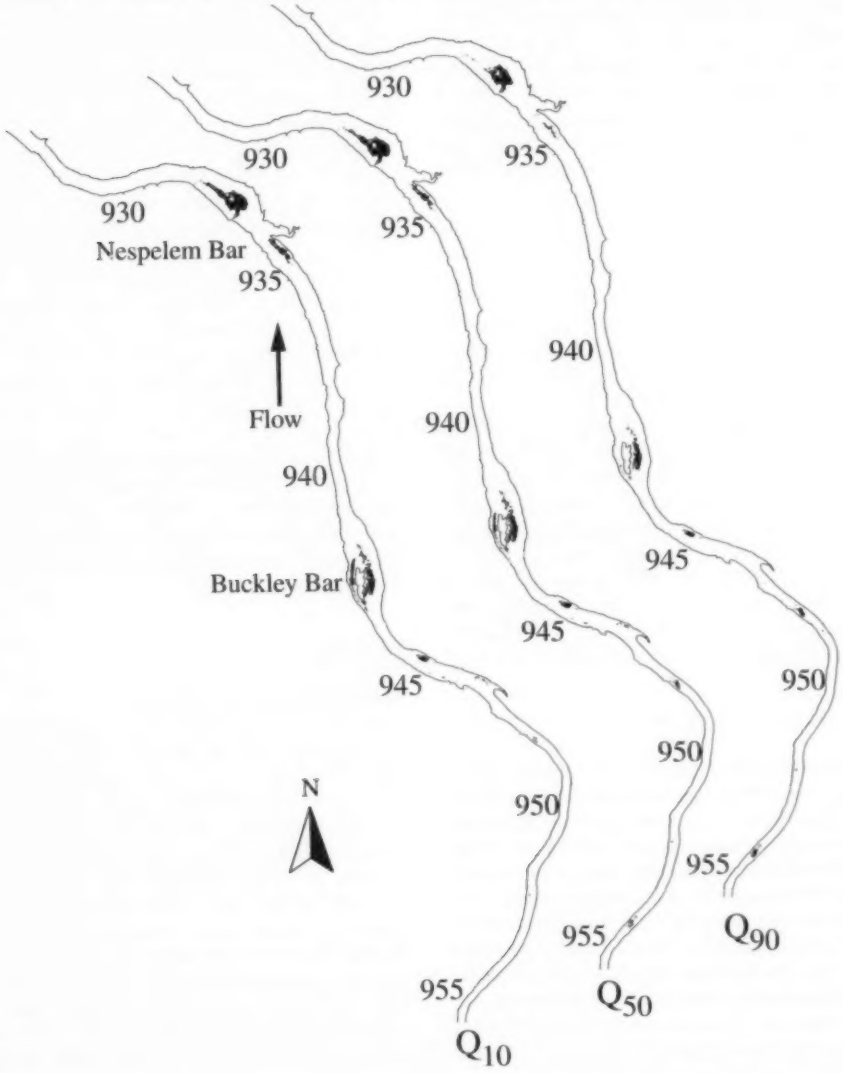
Table 2. Quantity of potential spawning habitat by discharge scenario, based on binary habitat modeling.

Discharge	Total area (ha)	Suitable (ha)	Not suitable (ha)	Suitable (%)	Not suitable (%)
Q_{10}	973.9	49.9	924.0	5.1	94.9
Q_{50}	971.6	48.7	922.9	5.0	95.0
Q_{90}	968.9	33.2	935.7	3.4	96.6

Fig. 2. Potential fall chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat (solid areas) in the upper reach of the Chief Joseph Reservoir on the Columbia River for the Q_{10}, Q_{50}, and Q_{90} discharges. Numbers adjacent to the channel indicate river kilometre (rkm).



discharge scenario, 74% of the potential spawning habitat was in water depths > 4.0 m, whereas 88% of those areas contained water velocities ≤0.75 m·s^{-1} (Fig. 4). The characteristic of relatively deep, slow water within the spawning habitat of the study area was generally applicable to all potential spawning areas.

The hydraulic modeling results for the entire study area (i.e., not just within potential spawning habitat) indicated that depth is much more of a limiting factor of potential spawning habitat than water velocity. Under the Q_{50} discharge scenario, the water depth in 62% of the study area was outside the fall chinook spawning habitat criteria, whereas 61% of the study area was deeper than 9.5 m. Water velocities (Q_{50}) in 29% of the study area were outside the criteria, with only 0.1% of the study area containing velocities greater than 2.25 m·s^{-1}.

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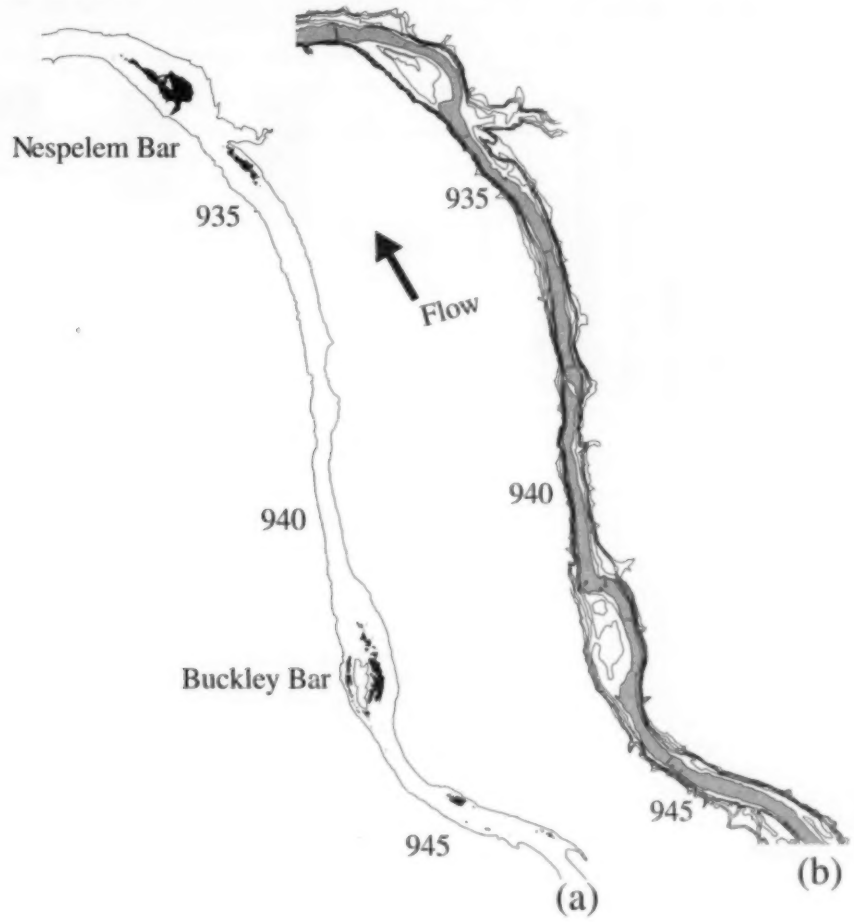
Fig. 3. (*a*) Potential fall chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat (solid areas) for the Q_{50} discharge and (*b*) relationship to before-dam channel morphology in the upper reach of the Chief Joseph Reservoir on the Columbia River. The before-dam topographic maps were produced by the U.S. Geological Survey in 1930 with a contour interval of approximately 6 m. The before-dam river channel in (*b*) is shaded.



The estimates of CI for the potential spawning habitat produced similar results. Under the Q_{50} discharge scenario, 64% of the potential spawning habitat had a CI value ≤0.50, or less than half the optimal index value of 1.0 (Table 3; Fig. 5). High quality habitat (CI > 0.76) accounted for 20% (9.6 ha) of the total potential spawning habitat. Approximately 50% of each spawning area had CI values ≤0.50.

Redd capacity

Our analysis of redd capacity within the potential spawning habitat resulted in a large range of redd numbers, depending on the calculation method used. Using average redd sizes alone (i.e., no inter-redd spacing, high concentrated spawning) applied to the reduced potential spawning habitat area of the Q_{50} discharge resulted in estimates ranging from 1058 to 6951 redds required to fill the given habitat area (Table 4). That estimate was reduced to 207–1599 redds when accounting for the average area used for a redd, including inter-redd spacing (Table 4).

The analysis of redd capacity based on the relative suitability (i.e., the CI) of the potential spawning habitat resulted in a similarly large range of redd numbers. Using average redd sizes alone (i.e., no inter-redd spacing, high concentrated spawning) applied to the total potential spawning habitat area within the CI range of 0.76–1.0 (i.e., high quality) under the Q_{50} discharge resulted in estimates ranging from 4169 to 4566 redds (Table 5). When factoring in the average area used for a redd, including inter-redd spacing, the capacity estimate was reduced to 818–1051 redds required to fill the potential spawning habitat under the Q_{50} discharge scenario (Table 5).

Discussion

The results from the modeling of potential fall chinook salmon spawning habitat availability suggest that the primary limiting physical factors in the study area are the hydraulic characteristics of water depth and velocity. Some

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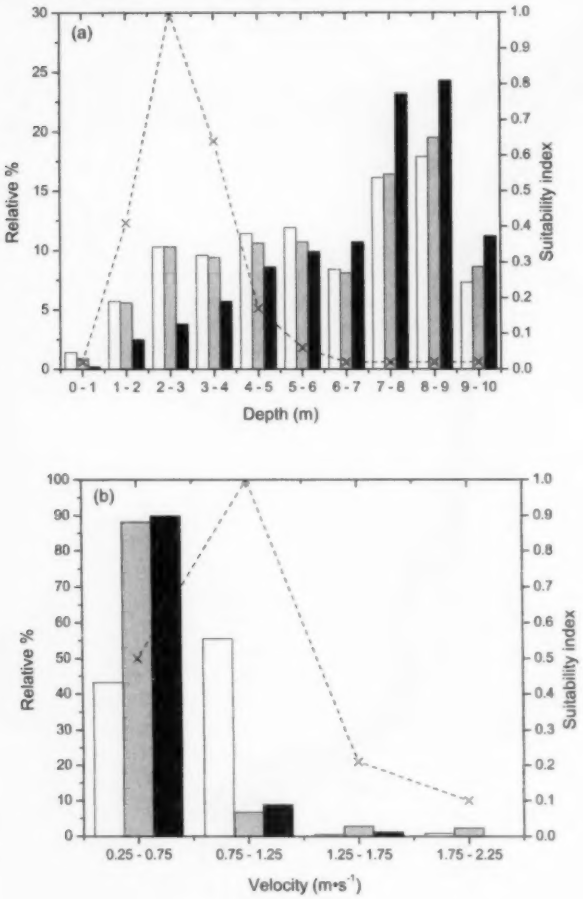
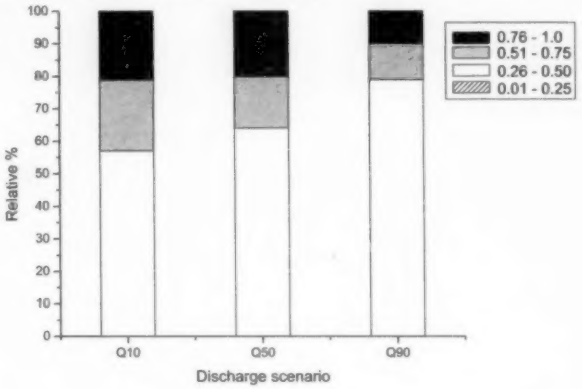
Fig. 4. (*a*) Depth and (*b*) velocity within suitable fall chinook salmon (*Oncorhynchus tshawytscha*) spawning areas for the Q_{10} (open bars), Q_{50} (shaded bars), and Q_{90} (solid bars) discharge scenarios. The fall chinook salmon spawning habitat suitability index (SI) is provided for reference (broken line).



researchers have suggested that water depth alone does not limit spawning habitat use by chinook salmon (Chapman et al. 1986). Although this may be true, studies of fall chinook spawning in the Columbia River have not documented redds deeper than 9.1 m (Chapman et al. 1986; Swan 1989), and researchers in the Snake River noted that no fall chinook salmon redds were deeper than 6.5 m, even though searches for redds in suitable habitat frequently occurred in deeper water (Groves and Chandler 1999). One reason for a depth threshold may be that visual cues related to mate recognition and substrate differentiation are reduced at depths greater than light penetration levels (Geist and Dauble 1998).

Potential spawning habitats were dominated by water depths on the deeper end of the suitable range and water velocities toward the slower end of the suitable range. In contrast, within a major spawning area of the Hanford Reach, 80% of the habitat within fall chinook salmon redd clusters contained water velocities of 1.4–2.0 m·s^{-1} and water depths of 2.0–4.0 m (Geist et al. 2000). Additional data from Hanford

Fig. 5. The composite suitability index (CI) of potential fall chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat in the upper reach of the Chief Joseph Reservoir on the Columbia River. CI = 0.76–1.0, solid bars; CI = 0.51–0.75, shaded bars; CI = 0.26–0.50, open bars; no habitat fell into the category of CI = 0.01–0.25. The relative percent of composite index quartiles is given for three modeled discharge scenarios.



Reach redds indicate that only 10.5% of the 230 redds were constructed in water depths >4.0 m, whereas 29% of those redds were located in water velocities ≤0.75 m·s^{-1}. Conversely, 43% of the redds were in water depths between 2 and 3 m, and 58% of the redds were in areas of the water velocities from 0.75 to 1.25 m·s^{-1}. Fall chinook salmon redds in the Snake River were observed in an average water depth of 2.8 m and average water velocity of 1.1 m·s^{-1}. In deepwater fall chinook salmon spawning habitat in the Columbia River, near-bottom water velocities at redds averaged 1.75 m·s^{-1} (Swan 1989) and 0.93 to 1.13 m·s^{-1} over a range of discharges (Chapman et al. 1986).

Although channel-bed substrate is not a primary limiting factor of fall chinook spawning habitat within the study area, it is likely a contributing factor largely because of hydraulic conditions rather than grain size composition. Hydraulic conditions within the potential spawning areas are likely not sufficient to initiate channel-bed movement or to sustain periodic sediment transport and deposition necessary to maintain a substrate matrix suitable for salmonid spawning. Although we characterized the overall grain size distribution of each geomorphic unit, we did not map small-scale changes in substrate composition within a sampling unit. Site-scale evaluations of geomorphic competency (e.g., sediment transport), substrate quality (e.g., permeability, percent fines), and surface water – groundwater interactions (e.g., vertical hydraulic gradient) would be required to further evaluate habitat quality of potential spawning sites.

Our estimates of potential spawning habitat result from the combined use of two-dimensional (2D) hydraulic modeling (River2D) and GIS, both of which may lead to some uncertainty in the estimates. Among practitioners of riverine habitat modeling, 2D models (i.e., depth-averaged) are generally considered to result in better estimates of hydraulic conditions within a river channel than one-dimensional (1D, i.e., cross section averaged) models (Leclerc et al. 1995; Hardy 1998; Lane 1998). Although the daily range of Grand

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Table 3. Composite index (CI) of potential spawning habitat for all discharge scenarios.

	Discharge scenario modeled					
	Q_{10}		Q_{50}		Q_{90}	
Composite index (CI)	Relative %	Area (ha)	Relative %	Area (ha)	Relative %	Area (ha)
0.01–0.25	0	0.0	0	0.0	0	0.0
0.26–0.50	57	28.4	64	31.1	79	26.3
0.51–0.75	22	10.9	16	7.9	11	3.7
0.76–1.0	21	10.6	20	9.6	10	3.2

Table 4. Redd capacity of potential fall chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat based on redd sizes and inter-redd spacing for the Q_{50} discharge scenario.

	Percentage use of total suitable area (ha)					
	5% (2.4)	10% (4.9)	15% (7.3)	20% (9.7)	25% (12.2)	30% (14.6)
Redd size (m^2)						
21	1158	2317	3475	4634	5792	6951
23	1058	2115	3173	4231	5288	6346
Area used (m^2)						
91	267	533	800	1066	1333	1599
117	207	415	622	830	1037	1245

Note: Redd capacity is defined as the total number of redds required to fill a given area of potential spawning habitat, reduced by 5–30% to reflect proportional utilization. The area used for a redd was estimated at 91 m^2 and 117 m^2 based on a 21-m^2 redd plus 2.8-m inter-redd spacing and a 23-m^2 redd plus 3.4-m inter-redd spacing, respectively.

Table 5. Redd capacity of highly suitable (composite index (CI), 0.76–1.0) potential fall chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat based on redd sizes and inter-redd spacing.

	Q_{10}	Q_{50}	Q_{90}
Redd size (m^2)			
21	5035	4566	1506
23	4597	4169	1375
Area used (m^2)			
91	1159	1051	347
117	902	818	270

Note: Redd capacity is defined as the total number of redds required to fill a given area of potential spawning habitat. The area used for a redd was estimated at 91 m^2 and 117 m^2 based on a 21-m^2 redd plus 2.8-m inter-redd spacing and a 23-m^2 redd plus 3.4-m inter-redd spacing, respectively.

Coulee Dam discharge is large (e.g., 566–4245 $m^3 \cdot s^{-1}$), the median hourly discharge (Q_{50}) was representative of hydraulic conditions within the study area during the October–November time period. The use of exceedence discharges for modeling habitat availability ignores hydraulic conditions that change as a result of daily dam operations (e.g., the rate of water velocity change). However, in the absence of empirical data on the effects of such operations on fall chinook salmon spawning habitat selection, the use of exceedence discharges is the preferred approach. The 2D modeling of each discharge scenario (Q_{10}, Q_{50}, Q_{90}) continued until the hydraulic results were considered very good (i.e., mass balance convergence was achieved), as indicated by very low solution change between model time-step iterations and a net outflow less than 1% of the total discharge (Ghanem et al. 1995, 1996; Waddle et al. 2000). The most important input parameter for 2D models is the river bathymetry. We feel that the bathymetry surface created for this study is a very good model of the actual channel topography, although the averaging required to create the model results in some loss of fine-scale elevation detail.

Uncertainties in our estimates of potential habitat arise from the suitability criteria used for defining suitable spawning habitat (binary model) and from the suitability index (SI) curves used for calculating composite suitability (CI) of a spawning area. The suitability criteria for depth, velocity, substrate, and channel-bed slope were compiled from studies of most major fall chinook salmon spawning areas within the mainstem Columbia and Snake rivers (reviewed in Geist and Dauble 1998; Groves and Chandler 1999; Geist et al. 2000). Although the SI curves represent the best available information to date, it is not known in what proportion fall chinook salmon selected spawning areas with these microhabitat characteristics (i.e., depth–velocity combinations) relative to the total availability of microhabitat. Nevertheless, we believe that our estimates of potential spawning habitat were within acceptable ranges, particularly as they incorporated multiscale geomorphic characteristics of the study area.

Estimating the redd capacity of a river reach based on potentially suitable habitat leads to a high degree of uncertainty. Much of the variability in habitat and capacity estimates may result from a general lack of understanding of the habitat conditions influencing fall chinook salmon spawning site selection. Observations from studies in the Columbia and Snake rivers indicate that spawning fall chinook salmon utilize a relatively small proportion of seemingly suitable habitat within a contiguous area (Dauble and Watson 1990; Geist and Dauble 1998; Geist et al. 2000). Our estimates of redd capacity based on proportional use of suitable spawning habitat (i.e., 5–30%) effectively account for this fact and produce redd capacity estimates consistent

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with these observations, particularly when factoring in the total area used for an individual redd (i.e., redd size plus inter-redd spacing). Our redd capacity estimates compare favorably with those observed in other mid-Columbia fall chinook salmon spawning populations. When applying the habitat model to a fall chinook salmon spawning area downstream of Wanapum Dam in the Columbia River, observed habitat use ranged from 5 to 30% of the total suitable spawning habitat (McMichael et al. 2002). Estimating production potential (i.e., redd capacity) based on proportions of potentially suitable habitat provides a starting point for management discussions of reintroducing fall chinook salmon upstream of Chief Joseph Dam.

Current escapement of ocean-type (summer/fall) chinook salmon to the upper Columbia River provides a context for potential future escapement to the study area. The total number of adult fall chinook salmon migrating upriver of Wells Dam (the nearest Columbia River hydroelectric project downstream of Chief Joseph Dam) has averaged around 5700 annually over the past 5 years. Generally, redd counts in tributaries within the Methow and Okanogan basins follow the same trend as adult counts at Wells Dam, suggesting a lack of mainstem spawning. Redd counts ranged from 308 to 728 during the period from 1989 to 1993 for the Methow and Okanogan basins, translating into 6–10 adults per redd during this same time period (Chapman 1994), which is a similar fish per redd ratio to that of other fall chinook salmon spawning areas (Dauble and Watson 1997; Groves and Chandler 1999). Our estimates of redd capacity in the study area would represent at least a twofold increase in the fall chinook salmon redd capacity upstream of Wells Dam. The extent to which the added redd capacity is seeded depends on escapement to Chief Joseph Dam. Some fall chinook salmon are harvested during the Colville Confederated Tribes (CCT) fishery in the tailrace of Chief Joseph Dam. Annual harvest for this fishery was estimated as between 210 to 1095 summer/fall chinook salmon (average = 484) from 1980 to 2000 (Chris Fisher, Fish and Wildlife Department, CCT, P.O. Box 862, Omak, WA 98841, personal communication). These fish may be available for mainstem spawning in the study area, assuming that they are not "strays" destined for tributary spawning areas. However, it is evident that the current run size to Chief Joseph Dam would have to be increased significantly for full seeding of potential spawning areas to occur.

We estimate that under typical October–November flows, 5% (48.7 ha) of the study area contains potentially suitable fall chinook salmon spawning habitat within two primary areas, Buckley Bar and Nespelem Bar. This habitat is limited primarily by water too deep and secondly by water velocities too low, the combination of which results in 20% (9.6 ha) of the suitable habitat being characterized as high quality. Conservative estimates of redd capacity within the potential spawning habitat (48.7 ha) range from 207 to 1599 redds, based on proportional use of potential habitat and varying amounts of channel bed used for redds (redd size plus inter-redd spacing). Estimates of redd capacity within high quality spawning habitat (9.6 ha) range from 818 to 1051 redds, or similar to the upper range of conservative estimates of redd capacity. Estimates of the quantity and quality of potential spawning habitat could be refined if smaller-scale habitat features (e.g., vertical hydraulic gradient, substrate permeability, and sediment transport) were incorporated into the model. Nevertheless, the results of our study provide significant insight into one component of the complex issue of reintroducing anadromous fish to the Columbia River upstream of Chief Joseph Dam.

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Temperature and salinity effects on strontium incorporation in otoliths of larval spot (*Leiostomus xanthurus*)

Gretchen Bath Martin, Simon R. Thorrold, and Cynthia M. Jones

Abstract: Temperature dependence of strontium/calcium (Sr/Ca) ratios in foraminiferal calcite and coral aragonite is well established; however, factors controlling Sr/Ca ratios in fish otoliths remain obscure. To assess temperature dependence of Sr/Ca in marine fish otoliths, we reared spot (*Leiostomus xanthurus*) larvae under controlled temperature (17–26 °C) and salinity (15‰ and 25‰). We found a significant linear relationship between temperature and Sr/Ca ratios, with a sensitivity of approximately 5%·°C^{-1}. Otolith Sr/Ca values were also significantly higher at a salinity of 25‰ vs. 15‰, after accounting for differences in dissolved Sr/Ca ratios in the ambient water, with a sensitivity of approximately 1%/salinity (‰). These observations complicate the use of Sr/Ca ratios to determine temperature histories of spot larvae, because accurate temperature reconstructions are possible only with a priori knowledge of both ambient salinity and dissolved Sr/Ca ratios. Fully marine species residing in oceanic waters will not experience significant salinity variations; therefore, otolith Sr/Ca ratios may be useful recorders of temperature exposure. Otolith Sr/Ca thermometry in coastal fish species that make regular excursions into estuarine waters will be more problematic. Multiple geochemical tracers, including oxygen stable isotopes and other trace elements, may be necessary to accurately reconstruct temperature and salinity histories in these species.

Résumé : Il est bien démontré que les rapports strontium/calcium (Sr/Ca) dans la calcite des foraminifères et l'aragonite des coraux sont dépendants de la température; cependant, les facteurs qui contrôlent les rapports Sr/Ca dans les otolithes des poissons restent incertains. Afin d'évaluer le lien entre la température et les rapports Sr/Ca dans les otolithes de poissons marins, nous avons élevé des larves du tambour croca (*Leiostomus xanthurus*) dans des conditions contrôlées de température (17–26 °C) et de salinité (15 ‰ et 25 ‰). Il existe une relation linéaire significative entre la température et les rapports Sr/Ca, avec une sensibilité d'environ 5 %/°C. Les valeurs de Sr/Ca sont aussi significativement plus élevées à la salinité de 25 ‰ qu'à 15 ‰, une fois les différences des rapports de Sr/Ca dissous dans l'eau ambiante prises en compte, avec une sensibilité d'environ 1 %/salinité (‰). Ces observations rendent plus complexe l'utilisation des rapports Sr/Ca pour reconstituer l'histoire thermique des larves du tambour croca, parce que des reconstitutions précises de la température ne sont possibles que si la salinité ambiante et les rapports de Sr/Ca de l'eau sont connus d'avance. Puisque les espèces totalement marines habitant les eaux océaniques ne subissent pas de variations significatives de salinité, les rapports Sr/Ca de leurs otolithes peuvent être d'utiles témoins de leur exposition à la température. La thermométrie à l'aide du rapport Sr/Ca des otolithes chez les espèces côtières de poissons qui font des incursions régulières dans les eaux saumâtres pose plus de problèmes. L'utilisation de multiples traceurs géochimiques, dont les isotopes stables d'oxygène et d'autres éléments traces, peut s'avérer nécessaire pour arriver à reconstituer l'histoire de l'exposition à la température et à la salinité de ces espèces.

[Traduit par la Rédaction]

Introduction

Inspired by Odum's (1951*a*, 1951*b*) and Turekian's (1964) pioneering work on the biogeochemical cycling of strontium (Sr) in marine environments, scientists have used strontium concentrations of marine-carbonate structures to infer temperatures of present and past marine environments. Strontium thermometry based on aragonite in coral skeletons may reveal temperature variation in marine environments over annual to millennial time scales (e.g., Beck et al. 1992; Alibert and McCulloch 1997). Several studies have also suggested that Sr deposition in the calcite tests of marine foraminifera may be temperature-dependent (e.g., Elderfield et al. 1996; Lea and Martin 1996; Lea et al. 1999). Similarly,

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strontium/calcium (Sr/Ca) ratios in aragonite mollusc shells have been used to discern temperature and salinity variability in estuarine environments (Dodd and Crisp 1982; Stecher et al. 1996).

The geochemistry of otolith aragonite may also record temperature and elemental composition of ambient environments (Campana 1999). Otoliths are metabolically inert calcium carbonate structures formed by concentric daily growth increments in teleost fishes (Campana and Neilson 1985; Jones 1986). The chemical composition of otoliths may, in turn, reflect that of the surrounding water (Farrell and Campana 1996; Milton and Chenery 2001), as modified by temperature (Thorrold et al. 1997; Bath et al. 2000). This observation has led to the development of applications using otolith chemistry in conjunction with the chronological properties of otoliths to retrospectively track larval-transport pathways through time (Tzeng and Tsai 1994; Thorrold et al. 1997). Otolith Sr/Ca values have also been used to examine transport pathways as a function of ambient temperature (Radtke 1989; Townsend et al. 1989; Gallahar and Kingsford 1996) or salinity (Kalish 1990; Halden et al. 1995; Secor et al. 1995).

Strontium ions have the same valence and a similar ionic radius as calcium ions and are readily incorporated into aragonite by solid substitution for Ca according to the following equation:

$$(1) \qquad Sr^{2+} + CaCO_3 \rightarrow SrCO_3 + Ca^{2+}$$

The amount of substitution is a function of the partition coefficient between aragonite and the fluid from which the Ca and Sr ions precipitate. In most otolith studies, the partition coefficient is expressed relative to the ambient water because of difficulties in measuring concentrations in the endolymphatic fluid surrounding the otolith (Bath et al. 2000; Milton and Chenery 2001; but see Kalish 1991). Therefore,

$$(2) \qquad [Sr/Ca]_{otolith} = D_{Sr}[Sr/Ca]_{water}$$

where D_{Sr} is the partition or distribution coefficient representing the ratio between the Sr/Ca of the calcium carbonate structure and ambient water (Morse and Bender 1990).

Strontium thermometry relies on the observation that the Sr/Ca partition coefficient is temperature-dependent. Because biogenic aragonite typically is not in thermodynamic equilibrium, the exact form of the temperature dependence is usually determined empirically. Laboratory and in situ studies have been used to validate the temperature dependence of D_{Sr} in aragonitic coral skeletons (e.g., Smith et al. 1979; Swart 1979; Shen et al. 1996). However, despite a number of apparently successful validation studies, there remains vigorous debate concerning the degree to which Sr levels in coral skeletons are affected by temperature compared with biological processes (e.g., presence of algal symbionts (Cohen et al. 2002)).

The relationship between temperature and Sr/Ca ratios in fish otoliths is likely to be even more complicated than in coral skeletons because the otolith is isolated from seawater by branchial, intestinal, and endolymphatic membranes. Proposed relationships between Sr/Ca and temperature include Sr/Ca ratios and temperature being positively correlated (Fowler et al. 1995; Arai et al. 1996), negatively correlated (Townsend et al. 1992), and uncorrelated (Gallahar and Kingsford 1996). It is not clear if these inconsistencies are a result of interspecific variations in Sr uptake as a function of temperature or by unspecified methodological artifacts in some or all of the experiments.

In one of the few studies to carefully constrain water chemistry and temperature, Bath et al. (2000) found a positive relationship between D_{Sr} and temperature. However, their experiment was designed to test the influence of water chemistry on otolith composition and only consisted of two temperature treatments at a constant salinity. The objectives in the present study were to resolve the temperature dependence of the Sr/Ca partition coefficient in larval spot (*Leiostomus xanthurus*) and to examine if the partition coefficient was also influenced by ambient salinity. Based on the results of Bath et al. (2000), we hypothesized that Sr/Ca ratios in larval spot otoliths were a function of temperature but would not be affected by salinity after appropriate correction for the Sr/Ca ratio of the ambient water. If the relation between Sr/Ca and temperature is sufficiently predictive, this would allow for reconstruction of temperature histories from individual spot larvae. Such reconstructions could, in turn, provide information on larval-dispersal pathways that would be difficult, if not impossible, to gather using conventional approaches.

Materials and methods

Spot (*Leiostomus xanthurus*) were spawned and hatched on 10 December 1999 at the NOAA, National Ocean Service, Center for Coastal Fisheries and Habitat Research in Beaufort, North Carolina. Larvae were reared in a common tank in natural seawater at 34‰ salinity for 42 days, at which time they were randomly distributed among 24 acid-washed 20-L high-density polyethylene tanks at a density of 2 fish·L^{-1}. Fish were acclimated to the experimental treatments for a week before initiating the experiment to ensure adequate survival of the experimental fish. The 12 h light – 12 h dark cycle was controlled for the duration of the experiment. The fish were fed an artificial diet (Golden Pearls, 300–500 and 500–800 µm, Brine Shrimp Direct, Inc., Ogden, Utah) twice daily ad libitum.

Experimental tanks were randomly assigned two salinity treatments (15‰ and 25‰) and four temperature treatments (17, 20, 23, and 26 °C). Three replicate tanks were used for each treatment combination (24 tanks in total). Room temperature was maintained at 16 °C, and aquarium heaters were used to regulate temperatures within individual tanks. Artificial seawater (Instant Ocean®; Aquarium Systems Inc., Mentor, Ohio) mixed with deionized water was used to regulate salinity. Water was changed at 50% volume daily to maintain water quality and salinity.

Water samples from each tank were collected every third day and were filtered through 0.22 µm cellulose nitrate membrane filters, acidified with 40% trace metal grade HCl to pH 2, and then stored frozen for subsequent analysis. Water temperature, salinity, and pH were also recorded daily (Table 1). After termination of the experiment, all surviving fish were measured and frozen in individual plastic bags.

Sagittal otolith pairs were removed from the fish and scraped clean with acid-washed glass probes in a class-100 clean

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Table 1. Summary of mean water temperature (Temp.,°C, ±standard error (SE)), salinity treatment (Sal., ‰), [Sr] ($\mu g \cdot g^{-1}$, ±SE), [Ca] ($\mu g \cdot g^{-1}$, ±SE), dissolved Sr/Ca ([Sr/Ca]; $mmol \cdot mol^{-1}$, ±SE), number of otoliths analyzed (n), mean otolith mass (OM; mg, ±SE), and somatic growth rate (GR; $mm \cdot day^{-1}$, ±SE) within each of the 24 tanks during the course of the experiment.

Tank No.	Temp.	Sal.	[Sr]	[Ca]	[Sr/Ca]	n	OM	GR
9	17.5±0.1	15	7.87±0.43	234±16.9	15.5±0.35	7	0.95±0.23	0.47±0.04
11	18.1±0.1	15	6.92±1.73	199±49.4	15.8±0.28	7	0.99±0.19	0.46±0.03
20	18.5±0.1	15	6.89±0.54	188±15.6	16.8±0.85	8	0.62±0.08	0.31±0.02
24	20.1±0.1	15	6.72±1.68	200±50.5	15.6±0.43	8	0.71±0.21	0.36±0.02
5	20.8±0.1	15	7.25±0.79	203±23.8	16.5±1.02	7	0.99±0.29	0.45±0.04
18	21.2±0.2	15	8.57±0.50	253±11.8	15.5±0.30	8	0.88±0.14	0.42±0.02
10	22.7±0.3	15	6.87±0.42	199±14.2	15.9±0.44	8	1.21±0.18	0.52±0.02
21	23.4±0.2	15	8.10±0.58	235±15.3	15.8±0.41	8	1.13±0.23	0.48±0.03
22	23.8±0.4	15	7.33±0.22	216±11.9	15.6±0.39	8	0.79±0.27	0.37±0.03
4	26.1±0.2	15	7.81±0.45	223±10.8	16.1±0.69	8	1.21±0.29	0.50±0.04
14	26.2±0.2	15	8.42±0.47	246±12.3	15.6±0.21	8	0.96±0.23	0.42±0.03
16	26.8±0.2	15	7.36±1.05	215±31.1	15.7±0.16	8	1.24±0.20	0.50±0.02
1	17.5±0.1	25	10.33±0.91	334±39.1	14.4±0.67	8	0.61±0.26	0.32±0.02
7	17.8±0.1	25	11.23±0.68	366±14.2	14.0±0.65	4	0.79±0.20	0.31±0.03
15	18.7±0.1	25	10.25±1.04	332±41.9	14.3±0.60	8	0.54±0.13	0.28±0.02
2	19.9±0.1	25	12.12±1.32	382±52.8	14.7±0.62	8	0.69±0.24	0.30±0.02
8	20.2±0.0	25	10.89±1.01	356±27.2	14.0±0.71	8	0.63±0.22	0.26±0.03
6	20.3±0.0	25	10.68±0.25	349±22.8	14.1±0.78	8	0.70±0.19	0.34±0.02
23	23.2±0.0	25	11.53±0.83	376±20.5	14.0±0.70	8	0.94±0.36	0.43±0.05
12	23.3±0.4	25	12.19±0.41	382±17.0	14.7±0.54	7	1.03±0.36	0.43±0.05
13	23.5±0.3	25	13.17±0.66	410±21.1	14.7±0.37	8	0.88±0.18	0.39±0.02
19	25.6±0.2	25	12.60±0.69	406±14.0	14.2±0.45	8	0.91±0.31	0.39±0.05
3	25.8±0.4	25	10.44±1.64	321±40.8	14.7±0.55	1	0.88	0.33
17	26.3±0.1	25	11.58±1.36	371±34.9	14.2±0.52	6	1.06±0.27	0.44±0.04

room. Otoliths were ultrasonically cleaned in Milli-Q water (Millipore Corp., Billerica, Mass.) for 7 min and triple rinsed with ultrapure H_2O_2 (Ultrex; J.T. Baker (Mallinckrodt Baker, Inc.), Phillipsburg, N.J.), followed by three sequential rinses of Milli-Q water. Otoliths were then placed on acid-washed glass slides to dry for 36 h under a class-100 laminar-flow hood. After drying, otoliths were individually weighed to the nearest 10 µg and transferred to acid-washed 1.5-mL high-density polyethylene vials.

Otoliths from fish archived at the start of the experiment (n = 12) were also removed and weighed to determine the proportion of otolith material in the experimental fish deposited during the initial larval rearing. Otoliths from two to four fish were pooled for each of three samples to assure adequate masses for analyses, decontaminated, and then assayed using the approach outlined below. The mean Sr/Ca ratio from the pooled samples (n = 3) of preexperimental otoliths was 3.0 ± 0.2 $mmol \cdot mol^{-1}$.

Otoliths from a maximum of eight fish were randomly selected from each tank and prepared for Sr/Ca analysis by inductively coupled plasma mass spectrometry (ICP-MS). If the total number of remaining fish in the tank after the experimental period was less than eight, all remaining fish in the tank were used (see Table 1 for fish numbers per tank). Otoliths were dissolved in 70% ultrapure nitric acid (Ultrex; J.T. Baker) and then diluted to achieve a total dissolved solid concentration of 0.1 $mg \cdot g^{-1}$ in a 1% nitric acid solution. Otolith solutions were stored at 4 °C until the ICP-MS analysis. All analyses were run on a Thermo Finnigan Element 2 ICP-MS (Thermo Electron Corp., Waltham, Mass.) equipped with a self-aspirating (20 $\mu L \cdot min^{-1}$) PFA nebulizer and a dual-inlet quartz spray chamber. The method measured ^{48}Ca and ^{86}Sr in low resolution (R = 300) during a 2-min acquisition time (a total of 126 passes). Quantification of Sr/Ca ratios followed the procedure outlined by Rosenthal et al. (1999). All samples were standardized to a dissolved solution (0.1 $mg \cdot g^{-1}$) of an otolith reference powder with a certified Sr/Ca ratio of 2.782 $mmol \cdot mol^{-1}$ (Yoshinaga et al. 2000). The matrix of the standard was therefore matched to the dissolved Ca levels in the samples. An internal laboratory standard was run after each reference sample to estimate precision of the Sr/Ca method. The reference material was then treated as an unknown, and Sr/Ca values were determined as for individual samples above. Measured precision (percent relative standard deviation (% RSD), n = 34) of the Sr/Ca method was 0.06% (Fig. 1).

Analyses of water samples collected during the experiment were also conducted using ICP-MS. Four samples were run from each tank, including the start and end of the experiment and two others at 11-day intervals. All samples were spiked with Indium (In) (to 4.5 $\mu g \cdot g^{-1}$), which was used as an internal standard. The solutions were then aspirated into a Thermo Finnigan Element 2 ICP-MS, via a self-aspirating nebulizer (50 $\mu L \cdot min^{-1}$) and Scott double-pass spray chamber. Because of the presence of significant interferences on most of the Ca isotopes, ^{44}Ca, ^{88}Sr, and ^{115}In were measured in medium resolution (nominal R = 4500). Four samples from each tank were averaged and the mean values were then used in all subsequent analyses. To estimate precision of the water measurements, we determined Ca and Sr values

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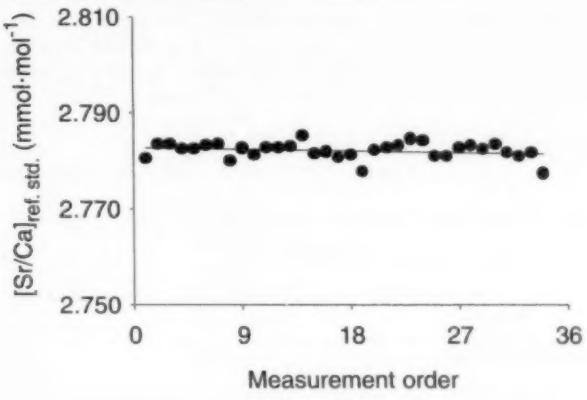
Fig. 1. Solution-based inductively coupled plasma mass spectrometer (ICP-MS) measurements of Sr/Ca values in an otolith certified reference material ($[Sr/Ca]_{ref.\ std.}$) plotted in run order through the two days of sample analyses. Overall precision across all runs (n = 34) was 0.06% relative standard deviation (RSD) in the reference material with a certified value of 2.782 mmol·mol^{-1} (Yoshinaga et al. 2000).



in a seawater reference material (seawater certified reference material (CRM); High Purity Standards, Inc., Charleston, S.C.). Our estimates of precision for both Ca and Sr concentrations in the seawater CRM was less than 2% RSD (n = 8). Partition coefficients (D_{Sr}) were calculated by dividing the Sr/Ca ratio measured in an otolith by the Sr/Ca ratio measured in the treatment tank water. Otolith Sr/Ca values from individual fish were averaged within tanks, and then the three tank averages were used as replicates for each of the eight treatments.

Analysis of covariance (ANCOVA) was used to test the influence of otolith precipitation rate on $[Sr/Ca]_{otolith}$. The influence of otolith precipitation rate was also tested by correlating otolith mass with Sr/Ca ratios within each of the 23 tanks of sufficient sample sizes. This provided a test of rate effects on Sr/Ca ratios because all fish within the tanks have experienced identical environmental conditions (Bath et al. 2000). ANCOVAs were also used to test the influence of somatic growth rate on $[Sr/Ca]_{otolith}$. Finally, the influence of somatic growth rate on otolith precipitation rate was tested by correlating growth rate with $[Sr/Ca]_{otolith}$ within each of the 23 tanks of sufficient sample sizes. Individual growth rates were calculated as the difference between the mean standard length (SL) of pooled fish at the beginning of the experiment and the SL of individual fish at the end of the experiment divided by the number of experiment days. The means of fish growth rates were calculated for individual tanks.

Two-way analysis of variance (ANOVA) was used to test for significant differences in $[Sr/Ca]_{otolith}$ and D_{Sr} among temperature and salinity treatments. Salinity and temperature were treated as independent categorical variables, and $[Sr/Ca]_{otolith}$ and D_{Sr} were treated as dependent variables in the analyses. The assumptions of ANOVA were met: residuals were normally distributed and homogeneous among factor levels. Finally, because temperature was a quantitative variable, we were able to test the significance of the relation between both $[Sr/Ca]_{otolith}$ and D_{Sr} with temperature using both linear and quadratic functions.

Results

We determined that conditions during the initial rearing period had little effect on the resultant otolith chemistry of the experimental fish because otoliths from these fish averaged less than 50 µg compared with a mean value of 890 µg for otoliths from fish at the end of the experiment. The Sr/Ca ratios of otoliths from 175 juvenile *L. xanthurus* ranged from 3.05 to 6.08 mmol·mol^{-1}, with an overall mean of 4.40 mmol·mol^{-1}. Water Sr/Ca values ranged from 11.91 to 19.36 mmol·mol^{-1}, with an overall mean of 15.09 mmol·mol^{-1}. Sr/Ca partition coefficients ranged from 0.20 to 0.43, with an overall mean of 0.29.

Biomineralization and growth rate effects

Using otolith mass as a proxy for aragonite precipitation rates, an ANCOVA demonstrated no significant effect of mean otolith mass among tanks on $[Sr/Ca]_{otolith}$ (F = 0.021, $p > 0.05$, n = 24). There was, however, significant variability in $[Sr/Ca]_{otolith}$ among tanks that were functions of temperature and salinity treatments and considerable variations in otolith mass among individual fish within tanks (Table 1). Because individual fish within a tank had experienced identical conditions, we also ran Pearson correlations between otolith mass and otolith Sr/Ca within each of 23 tanks. A total of 14 of 23 correlations were negative, but only three of 23 correlations were significant after Bonferroni correction for multiple tests. Somatic growth rates were, as expected, significantly affected by tank temperature (F = 4.52, $p < 0.05$, n = 24) and tank salinity (F = 11.43, $p < 0.05$, n = 24). An ANCOVA also demonstrated no significant effect of mean growth rates among tanks on $[Sr/Ca]_{otolith}$ (F = 0.016, $p > 0.05$, n = 24). Looking at the relation within tanks, Pearson correlations between growth rate and $[Sr/Ca]_{otolith}$ demonstrated that although 16 of 23 correlations were negative, only two of 23 correlations were significant after Bonferroni adjustment.

Water chemistry

Elemental concentrations of ambient water in the tanks were significantly different between salinity treatments (Fig. 2). As expected, both Ca and Sr were higher at 25‰ than at 15‰ ($[Ca]_{water}$, $|t|_{0.05,(2),22}$ = 14.62, $p < 0.05$; $[Sr]_{water}$, $|t|_{0.05,(2),22}$ = 11.85, $p < 0.05$). Water Sr/Ca ratios did not vary among temperature treatments but were significantly different between salinity treatments ($[Sr/Ca]_{water}$, $|t|_{0.05,(2),22}$ = 10.41, $p < 0.05$). Proportionately lower Ca concentrations relative to dissolved Sr in 15‰ salinity tanks led to higher Sr/Ca ratios in the low salinity treatment (Table 1; Fig. 2), presumably because Sr/Ca ratios were higher in the deionized water source than in the 25‰ salinity artificial seawater.

Otolith [Sr/Ca]

The two-way ANOVA model found a significant salinity and temperature effect on $[Sr/Ca]_{otolith}$ (Table 2). The interaction term was not significant (Table 2). A post-hoc Tukey multiple comparison showed significant differences among

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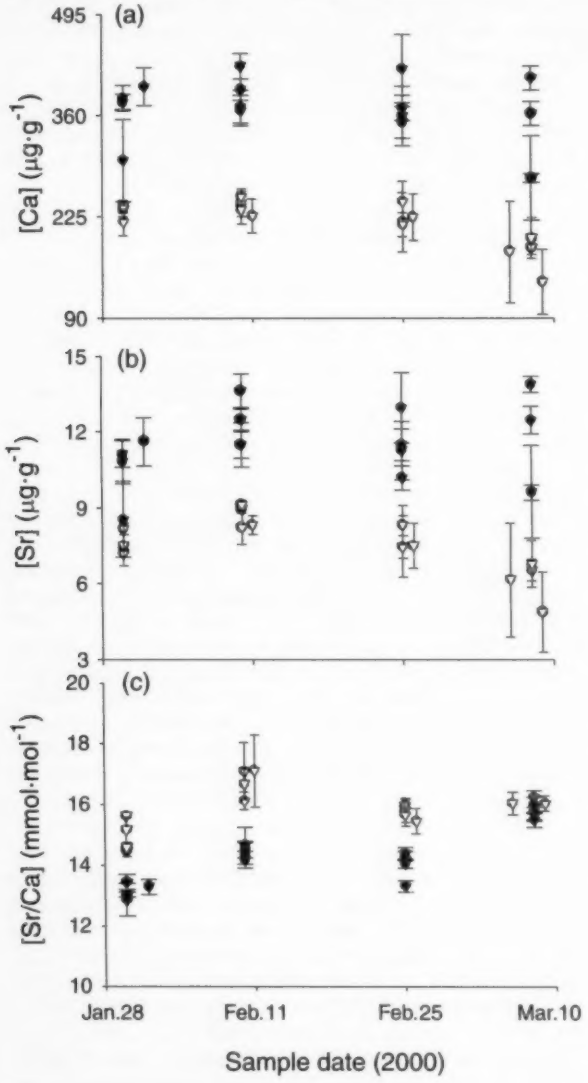

Fig. 2. Measured tank water (*a*) Ca and (*b*) Sr concentrations (μg·g^{-1}, ± standard error (SE)) by sample date for the duration of the experiment. (*c*) The calculated Sr/Ca ratio (mmol·mol^{-1}) in these water samples. The solid symbols represent the 25‰ salinity treatment tanks, and the open symbols represent the 15‰ salinity treatment tanks. Each of the four temperature treatments is represented by a different symbol shape: 17 °C (circles), 20 °C (triangles), 23 °C (squares), and 26 °C (diamonds).

all temperature treatments. There was also a significant linear, but not quadratic, relation between $[Sr/Ca]_{otolith}$ and temperature (Table 2; Fig. 3). At 25‰ salinity, the linear least-squares regression equation between $[Sr/Ca]_{otolith}$ and temperature ($r^2 = 0.95$, $n = 12$) was

$$(3) \quad [Sr/Ca]_{otolith} = 0.154 \pm 0.012(T\ (°C)) + 1.16 \pm 0.256\ (95\%\ \text{confidence interval})$$

For 15‰ salinity, the linear equation ($r^2 = 0.92$, $n = 12$) was

$$(4) \quad [Sr/Ca]_{otolith} = 0.179 \pm 0.017(T\ (°C)) + 0.348 \pm 0.382\ (95\%\ \text{confidence interval})$$

Sr/Ca partition coefficients

We detected significant salinity and temperature effects on Sr/Ca partition coefficients (Table 2), with a nonsignificant interaction between the two factors (Table 2). The linear function between D_{Sr} and temperature was significant, but the quadratic function was not (Table 2; Fig. 4). For 25‰ salinity, the linear least-squares regression equation between D_{Sr} and temperature ($r^2 = 0.90$, $n = 12$) was

$$(5) \quad D_{Sr} = 0.010 \pm 0.001(T\ (°C)) + 0.088 \pm 0.025\ (95\%\ \text{confidence interval})$$

For 15‰ salinity, the linear equation ($r^2 = 0.91$, $n = 12$) was

$$(6) \quad D_{Sr} = 0.012 \pm 0.001(T\ (°C)) + 0.013 \pm 0.026\ (95\%\ \text{confidence interval})$$

Discussion

Both $[Sr/Ca]_{otolith}$ and Sr/Ca partition coefficients increased linearly as a function of temperature over the ranges analyzed (17–26 °C). The temperature effect was not a result of differences in water chemistry among temperature treatments, as elemental concentrations and Sr/Ca ratios did not differ among temperature treatments. Presumably, there was no effect of diet, as all fish were fed the same food. Moreover, several experimental studies have found little evidence for an effect of diet on otolith Sr incorporation (Hoff and Fuiman 1995; Farrell and Campana 1996; Milton and Chenery 2001). We cannot eliminate physiological differences when such differences are correlated with growth because there was a significant effect of temperature on growth rate. However, aragonite precipitation rates and larval growth rates within individual tanks were in most cases not significantly correlated with Sr/Ca ratios in otoliths. Temperature was therefore the dominant variable controlling Sr/Ca ratios in the otoliths of larval spot in our experiment.

Bath et al. (2000) provided a first-order approximation of the temperature partition coefficient relation for larval spot, *L. xanthurus* (18–32.6 mm SL, mean = 24.2 mm SL):

$$(7) \quad D_{Sr} = 0.0046(T\ (°C) + 0.089 \quad (r^2 = 0.62)$$

Two points are worth noting with respect to the results of our earlier study. First, Bath et al. (2000) reported Sr/Ca partition coefficients that were significantly lower at a given temperature (0.18 at 20 °C, 20‰) than what we found in the present study (0.26 at 20 °C, 15‰; 0.30 at 20 °C, 25‰). The intercept of the linear regression between D_{Sr} and temperature (for the 20 and 25 °C treatments) was statistically indistinguishable between the two experiments. However, the temperature sensitivity of the relation between D_{Sr} and temperature in the present study (~5%·°C^{-1}) was approximately twice that reported by Bath et al. (2000) (~2%·°C^{-1}). Larvae were reared at two temperatures in the earlier study (20 and 25 °C). It is possible, therefore, that Bath et al. (2000) underestimated the temperature dependence because of a lack of temperature treatments. It is more difficult to reconcile the different estimates of D_{Sr} between the two

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Table 2. *Leiostomus xanthurus*. Analysis of variance (ANOVA) table summarizing the effect of salinity and temperature treatments on otolith [Sr/Ca] and the Sr distribution coefficient (D_{Sr}), along with significance tests of linear and quadratic contrasts between temperature and otolith [Sr/Ca] and temperature and D_{Sr}.

Source	SS	df	MS	F	$p < F$
Otolith [Sr/Ca]					
Salinity	0.241	1	0.241	7.42	0.015
Temp	6.20	3	2.1	63.6	<0.001
Salinity × temperature	0.068	3	0.023	0.695	0.569
Error	0.520	16	0.032		
Linear	5.98	1	5.98	184	<0.0001
Quadratic	0.047	1	0.047	1.46	0.245
D_{Sr}					
Salinity	0.011	1	0.011	61.8	<0.0001
Temperature	0.027	3	0.009	52.2	<0.0001
Salinity × temperature	0.0004	3	0.000	0.78	0.524
Error	0.003	16	0.000		
Linear	0.026	1	0.026	151	<0.0001
Quadratic	0.0002	1	0.0002	1.17	0.295

Note: SS, sums of squares; df, degrees of freedom; MS, mean squares.

Fig. 3. Sr/Ca (mmol·mol^{-1}) ratios in otoliths of laboratory-reared *Leiostomus xanthurus* as a function of tank temperatures (°C) at two salinity levels: 15‰ (●) and 25‰ (○). The lines were fitted by linear least-squares regression for each of the salinity treatments.

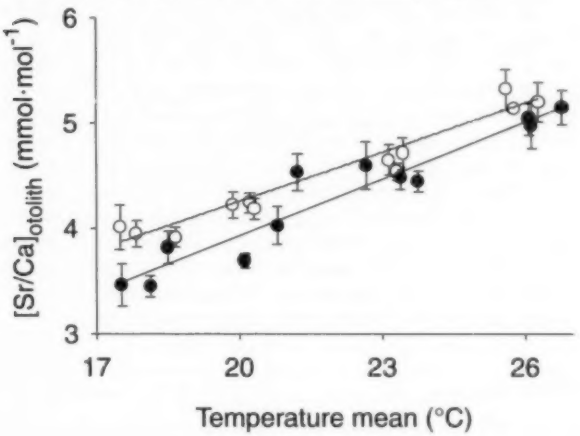
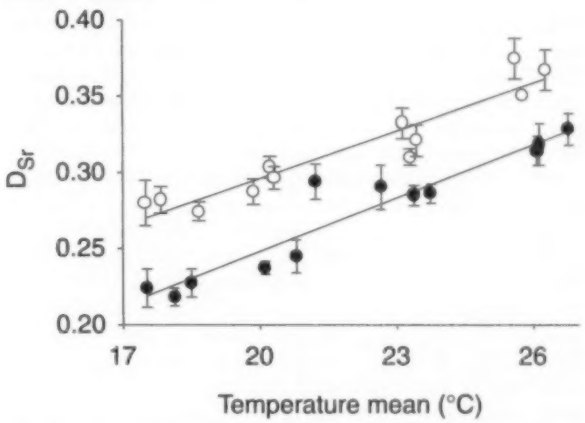


Fig. 4. Sr/Ca partition coefficients (D_{Sr}) for otoliths of laboratory-reared *Leiostomus xanthurus* as a function of tank temperatures (°C) at two salinity levels: 15‰ (●) and 25‰ (○). The lines were fitted by linear least-squares regression for each of the salinity treatments.



studies because both were based on multiple treatments with adequate levels of replication. We conclude that there are other factors influencing the magnitude of D_{Sr} in the otoliths of larval spot that remain to be identified.

The effect of temperature on Sr/Ca ratios in the otoliths of other fish species is ambiguous. Several studies have also shown positive effects of temperature on Sr incorporation into otoliths (Kalish 1989; Limburg 1995; Arai et al. 1996). Other researchers have suggested an inverse correlation between temperature and Sr/Ca ratios in otoliths (Radtke 1989; Sadovy and Severin 1992; Secor et al. 1995) or have been unable to detect any temperature dependence of $[Sr/Ca]_{otolith}$ (Gallahar and Kingsford 1996; Tzeng 1996; Chesney et al. 1998). Methodological problems may be responsible for at least some of these discrepancies, as few studies have adequately constrained $[Sr/Ca]_{water}$. The choice of analytical instrumentation may also be a factor, as most studies have used electron probe microanalysis (EPMA). The application of Sr/Ca thermometry, at least in coral skeletons, generally requires instrument precision of better than 0.5% RSD (Lea and Martin 1996). However, instrument uncertainty of Sr/Ca measurements in otoliths using EPMA is typically on the order of 5–10% (RSD) (e.g., Gunn et al. 1992; Campana et al. 1997). Precision of the Sr/Ca method using sector-field ICP-MS that we employed was 0.06% RSD, matching the best precision reported for instruments routinely used to determine Sr/Ca ratios in biogenic carbonates (Rosenthal et al. 1999; Schrag 1999). The increased precision of our estimates over earlier probe-based methods certainly increased our ability to detect relatively subtle, but predictable, effects of temperature on Sr/Ca ratios. We suspect that developmental stage may also influence Sr/Ca in otoliths. Kalish (1990)

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suggested that variations in Ca-binding proteins caused by changes in reproductive status influenced Sr/Ca ratios in otoliths of adult fish. Such regulation may then be less important in the larval stages that we examined compared with studies on older life history stages. Finally, it is likely that Sr and Ca uptake in otoliths is species-specific, and therefore a single relationship between Sr/Ca and temperature may not apply to all marine fish species.

Considerable debate also surrounds the temperature dependence of Sr/Ca partition coefficients in other biogenic carbonates. Most work has been conducted on the aragonite skeletons of hermatypic corals that typically demonstrate an inverse relation between D_{Sr} and temperature (Smith et al. 1979; Beck et al. 1992; Sinclair et al. 1998). Positive correlations have been identified between D_{Sr} and temperature in molluscs (Buchardt and Fritz 1978; Klein et al. 1996; Vander Putten et al. 2000) and calcitic foraminifera (Elderfield et al. 1996; Lea et al. 1999). Interestingly, Sr/Ca ratios of the aragonite from studies that documented a positive relation between D_{Sr} and temperature were considerably lower (<2.5 mmol·mol^{-1}) than that found in coral or sclerosponge aragonite (8–10 mmol·mol^{-1}). There may, therefore, be fundamentally different mechanisms generating the temperature dependence of Sr/Ca ratios between low Sr and high Sr aragonite. Stecher et al. (1996) and Purton et al. (1999) suggested that metabolic effects correlated with temperature led to positive correlations between Sr/Ca and temperature in bivalve and gastropod shells. We have been consistently unable to find correlations between otolith Sr/Ca and several proxies of metabolic rate (somatic and otolith growth) in individual spot larvae. Clearly more work in this area is needed, although we believe that there is now sufficient evidence to reject analogies between the temperature dependence of D_{Sr} in coral skeletons and fish otoliths.

More Sr was incorporated into larval spot otoliths at salinities of 25‰ than at 15‰, after accounting for differences in the Sr/Ca ratios of the rearing water. Dietary effects were unlikely to have caused the differences, following the argument outlined above for temperature. Rather, absolute Sr levels appeared to influence otolith Sr/Ca values beyond that predicted by $[Sr/Ca]_{water}$. Recent studies by Chowdhury and Blust (2001, 2002) provide a potential mechanism for our observations. They found that dissolved Ca and Sr in freshwater carp mutually inhibited uptake of ions across branchial and intestinal membranes. Positive, nonlinear inhibition of Ca ions by Sr ions at uptake sites on these membranes would, in turn, result in the observed effect of dissolved Sr on Sr/Ca ratios in otoliths.

The observation that Sr/Ca ratios in otoliths depend on temperature, $[Sr/Ca]_{water}$, and $[Sr]_{water}$ raises a number of potential problems for fish Sr thermometry. Both $[Sr/Ca]_{water}$ and $[Sr]_{water}$ must be constrained before temperature can be estimated from otolith Sr/Ca. Because Sr and Ca have long (~10^6 years) residence times in the world's oceans, fish that spend their entire lives in shelf or oceanic water masses will not experience significant variations in either $[Sr]_{water}$ or $[Sr/Ca]_{water}$. However, many fish species living in coastal waters are estuarine-dependent and traverse waters of variable water chemistry and temperature. Reconstruction of temperature histories will therefore require independent estimates of $[Sr]_{water}$ and $[Sr/Ca]_{water}$. Temperature and salinity are easy to measure and are frequently incorporated in sampling designs. Water strontium and calcium concentrations are rarely measured yet seem to be critical for the application of strontium thermometry to field-collected fish.

In summary, Sr/Ca ratios in the otoliths of larval spot are determined primarily by the physicochemical properties of the ambient water. When combined with the results of our earlier study (Bath et al. 2000), we conclude that temperature, $[Sr/Ca]_{water}$, and $[Sr]_{water}$ all have significant effects on otolith Sr/Ca ratios. In contrast, we saw no consistent evidence for metabolic effects on Sr/Ca ratios in otoliths, at least to the extent that metabolic rates are correlated with individual growth rates. Unfortunately, this does not mean that otolith Sr/Ca thermometry will be easy in estuarine-dependent fish species because independent geochemical tracers that constrain both $[Sr/Ca]_{water}$ and $[Sr]_{water}$ will need to be developed. For instance, both stable oxygen ($^{18}O/^{16}O$) and strontium ($^{87}Sr/^{86}Sr$) isotopes vary linearly with $[Sr]_{water}$ and $[Ca]_{water}$ in estuarine systems (Chesney et al. 1998; Thorrold et al. 1998). We suggest, however, that marine fishes that do not experience significant variations in $[Sr]_{water}$ and $[Ca]_{water}$ are logical species to test our ability to reconstruct temperature histories from Sr/Ca ratios in otoliths.

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Managing fishing power: the case of Alaska red king crab (*Paralithodes camtschaticus*)

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Abstract: Because of concern about the inability to manage the Bristol Bay red king crab (*Paralithodes camtschaticus*) fishery in Alaska and, in particular, to use in-season fishery performance to close the fishery at or near the preseason guideline harvest level, increasingly stringent pot limits were adopted to elongate the collapsing seasons. This paper provides a rigorous examination of the effect that pot limits had on season elongation and whether a redistribution of wealth occurred between large and small fishing vessels as a result of the policy. A simulation model of the fishery shows that pot limits did not elongate the season sufficiently to improve in-season management. Moreover, the policy allowed vessels to capture efficiency gains arising from an industry-wide reduction in fishing capacity. Both vessel size classes benefited from mutual gear reduction in all years except 1992. Redistribution of wealth was found to occur only in one year of the five years examined.

Résumé : L'incapacité de gérer la pêche commerciale du crabe royal du Kamchatka (*Paralithodes camtschaticus*) en Alaska et, en particulier l'impossibilité d'utiliser la performance de la pêche au cours de la saison pour mettre fin à la pêche au moment (ou près du moment) où les quotas de capture fixés avant la saison ont été atteints, ont généré beaucoup d'inquiétude. C'est pourquoi les gestionnaires ont adopté des restrictions sur le nombre de pièges de plus en plus rigoureuses pour allonger les saisons de pêche qui risquaient l'effondrement. Nous présentons ici un examen rigoureux de l'effet de ces restrictions sur l'allongement des saisons de pêche et nous vérifions s'il y a eu une répartition de la richesse entre les petits et grands navires de pêche en conséquence de cette politique. Un modèle de simulation de cette pêche commerciale montre que les limites de capture n'ont pas allongé suffisamment la saison de pêche pour améliorer la gestion au cours de la saison. De plus, la politique a permis aux navires de connaître des gains d'efficacité dus à une réduction de la capacité de pêche au sein de l'ensemble de l'industrie de pêche. Les deux classes de navires ont profité de leur réduction mutuelle d'engins de pêche, excepté en 1992. Une redistribution de la richesse ne s'est produite qu'une seule année pendant les cinq années de l'étude.

[Traduit par la Rédaction]

Introduction

Fishery managers often confront the dilemma of how to arrest collapsing stocks. This problem escapes few open-access fisheries, including those that are license-limited. Biological causes contributing to depressed stocks are rarely controllable, unless resulting from overharvest. Moreover, fundamental changes in management to market-based quota systems that potentially could protect stocks are politically difficult or impossible to implement and generally do not occur with the expedience required to protect collapsing stocks. Management naturally defaults to familiar command and control policies designed to attack the inimical effects of excessive fishing power. There are few or no other tools at the manager's disposal.

The efficacy of command and control fisheries management is necessarily predicated on two implicit beliefs. The controls are assumed to be effective. They also are implicitly assumed to yield social benefits from stock protection that exceed any policy-induced efficiency losses, though it is not uncommon for the management imperative to preempt any economic considerations. This paper examines the efficacy of one such effort to control fishing power in the Bristol Bay Alaska red king crab (*Paralithodes camtschaticus*) fishery.

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Because of concerns about the inability to manage the Bristol Bay red king crab fishery and, in particular, to use in-season fishery performance to protect the stock by closing the fishery at or near the preseason guideline harvest level (GHL), the Alaska Department of Fish and Game (ADFG), with approval from the Alaska Board of Fisheries (BOF), initiated a series of increasingly stringent pot limit policies designed to elongate the collapsing seasons by constraining the fishing power of the fleet. A uniform pot limit of 250 pots was first implemented in 1992. A court ruled this policy discriminatory against large vessels. The policy was changed to a two-tiered pot limit in 1993; vessels less than or equal 38.10 m in length (small vessels) were allowed to fish 200 pots, whereas vessels over 38.10 m (large vessels) were limited to 250 pots. More stringent limits were implemented in 1997, after the 1996 season when the GHL was exceeded by two-thirds in just 4 days. This new and ongoing regulation adjusts the pot limit depending on the GHL and fleet size. Notably, it reduces pot limits from 200–250 to 100–125 whenever the GHL lies between six and nine million pounds. The complete regulation is given in 5AAC 34.825 (h) (ADFG 1998). The alternative pot limits that applied during the 1991–1997 period are hereafter simply referred to as "none, 250, 200–250, and 100–125".

Concerns over the effectiveness of pot limits in elongating the season were raised as soon as they were first implemented. Greenberg and Herrmann (1994) provided an econometric analysis of potential impacts of pot limits considered by the BOF. The authors concentrated on the allocative consequences of pot limits, concluding that pot limits had the effect of reallocating harvest and wealth from large vessels to small vessels. However, they also found that pot limits were "only moderately effective" in elongating the season. The authors noted that a better understanding of fishing strategies and practices is necessary to determine the actual effect that pot limits have on overall fleet fishing power and season length.

Following a sequence of regulatory changes, the BOF directed ADFG to gather needed information to assess the remaining question of the effectiveness of the pot limit in elongating season length. To that effect, observers were placed on board during the 1997 and 1998 seasons. Using the collected data, Tracy et al. (1999) concluded that pot limits did not help managers predict season length or close the fishery at the GHL, again, because little is known about the effect of pot limits on individual fishing strategies and fleet fishing power.

Briand et al. (2001) addressed the issue from an entirely different perspective based on empirical estimation of year-specific individual catch-per-unit-effort (CPUE) functions for the 1991–1993 and 1996–1997 Bristol Bay red king crab fisheries (the fishery was closed in 1994 and 1995). Using a flexible functional form, they found that CPUE is an asymptotic function of soak time. Because pot limits surely impact soak time decisions, they speculated that the pot limit policy might have been counterproductive.

The primary objective of this paper is to address the need for a better understanding of whether pot limits achieved their season elongation policy objective and how pot limits differentially impact small- and large-vessel fishing strategies and economic performances. The speculation posited by Briand et al. (2001) that the pot limit policy failed to elongate the season is addressed in the context of a behavioral model that simulates how catcher vessels would operate to maximize economic returns, measured as quasi-rents (revenues in excess of variable costs), subject to alternative pot limit constraints. The alternative objective function of maximizing catch was investigated initially, with no change in the qualitative outcome regarding season length. Accordingly, we report only the findings under the more general assumption of quasi-rent maximization. Examining whether a redistribution of catch and quasi-rents from large to small fishing vessels occurred as a result of the pot limit policy is a secondary objective of the analysis. Potential efficiency gains, i.e., increase of quasi-rents for both large and small vessels, are also investigated.

The analysis abstracts from the myriad of vessel lengths, hull and power plant configurations, skipper and crew characteristics, and the related diverse fishing practices. Instead, this paper highlights general behavioral characteristics that distinguish a small vessel's response to pot limits from that of a large vessel, assuming both fish around the clock. This representative vessel approach allows a clear exposition of the basic strategic or behavioral differences between the two policy-defined size classes. No attempt is made at defining all vessel-specific strategies or corresponding optimal economic performances. The representative vessel approach, however, does enable one to examine relative economic performance under year-specific catch and policy conditions.

There is also a pragmatic reason for adopting the representative vessel approach. State and federal fishery regulations do not mandate collection of production cost data. Cost data used in this study were collected by the authors from a sample of small- and large-vessel owners who were willing to cooperate in developing a representative, a single small- and a single large-vessel cost of production profile, while operating under the constraint of maintaining confidentiality of individual vessel information. Insights into aggregate fleet fishing performance, season length, and distributional impacts of the pot limit policies were thus necessarily derived from representative vessel behavior.

A general intuitive description of methods used to simulate optimal behavior for the individual vessel and for the fleet is provided in the next section. Particular attention is given to model formation and implementation. Model details are provided in Appendix A. Simulation results are discussed in the final section.

Methods

The model of fishing behavior, with and without pot limits, is constructed in the context of a complete description of the fishing process and the year-specific incentives that harvesters have to adjust the fishing process. This model is conceptualized in a rational expectations context (Muth 1961). A vessel operator is assumed to form a season length expectation before the season to plan the fishing strategy, e.g., the number of pots to be fished during the fishing season and the length of time that the pots will soak. In reality, the season length expectation is based on a variety of factors, in-

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cluding the preseason GHL, fleet composition and size, and institutional constraints such as pot limits and market structure. If the season length expectations are correct, it is rational for the operator to follow the preseason plan. It is not essential that the vessel operator actually knows the season length in advance. The operator simply needs to behave as if it is known.

Rational expectations are modeled as a two-stage process. The first stage involves a quasi-rent maximization model in which the individual harvester is assumed to adopt the optimal fishing strategy for any given expected season length, independent of all other vessels. In this stage, individual decision variables include optimum amounts of gear and soak time that maximize quasi-rents, and this choice defines the individual vessel catch for an expected season length. Each harvester's optimization problem is subject to three generic constraints: (1) year-specific harvesting-efficiency conditions that are implied by the CPUE function; (2) relevant vessel characteristics, such as pot carrying capacity and variable cost structure; and (3) policy constraints concerning the maximum number of pots that a vessel may fish under alternative policy scenarios. The individual vessel behavior that maximizes a harvester's quasi-rents is simulated under alternative policy scenarios by imbedding the appropriate policy constraints in each harvester's optimization problem.

Optimal strategies of individual harvesters are brought into industry equilibrium in the second stage by imposing a common season length across all harvesters, aggregating fishing behavior across all vessels, and requiring that aggregate catch equals the observed historical fleet-level harvest in each year. Fishery season lengths under various policy alternatives ultimately are determined by the minimum fishing time required by the fleet to catch the historical yearly harvest levels. This aspect of the model incorporates the fishing market structure as a license-limited, open-access race for fish. It should be noted that race for fish encourages similar behavior among similar vessels. If any vessel operators were to ignore the time constraint, these individuals would forgo catch and quasi-rents to the benefits of all others who raced for fish.

The rest of this methods section provides an overview of the vessel optimization model. The purpose of this overview is to provide the reader with an intuitive appreciation of the optimization model; the detailed optimization model is presented in Appendix A. Initially, the model is portrayed in its most elemental characterization, which is expanded to accommodate the fishing process and the associated period-specific catch functions. The way in which this model assures an optimal solution is discussed in the final subsection.

Simplified optimization model

A general representation of the harvesters' constrained optimization problem follows:

$$(1)\qquad \max_{n^v, l^v, \mathrm{FT}^v} \{\mathrm{QR}^v = p(1-\alpha)\mathrm{CATCH}^V - \mathrm{VC}(n^v, l^v, \mathrm{FT}^v)\}$$

subject to $\mathrm{FT}^v \le \mathrm{SL}_{\mathrm{EXP}}$ and $n^v \le \min[\mathrm{PotLimit}^v, \mathrm{MaxPots}^v]$, where v denotes the vessel size (large or small boats), QR denotes quasi-rents retained by the vessel, p denotes the exvessel price of crab, α denotes the crew share, and CATCH is the total harvest by the vessel. The first term in the objective function is gross revenue to the vessel, net of crew share. The second term is the variable cost of fishing (VC), which is a function of the number of pots fished (n), the intensity of the fishing activity reflected by the number of times that pots are turned over during the fishing season (l), and the time that it takes the vessel operator to carry out the fishing plan (FT). $\mathrm{SL}_{\mathrm{EXP}}$ denotes the operator's preseason expectation of season length, which is an upper bound on the harvester planning horizon. The second constraint limits the number of pots (n) that the operator fishes to the lesser of the vessel size-specific pot limit (PotLimit) or the maximum number of pots that a vessel may fish (MaxPots). A large catcher is assumed to fish, at most, its vessel carrying capacity of 300 pots, whereas a small catcher is assumed to fish a maximum of 250 pots, twice its vessel carrying capacity made possible by the use of wet storage of 125 pots (described further in the next section).

This simplified model is subsequently expanded to the complete model of fishing behavior in Appendix A. The expansion involves defining the elements of eq. 1 (CATCH, VC, and FT). CATCH is defined by the CPUE function, which is a function of period-specific soak time. Soak time differs across periods because of the fishing process, described in the next section. VC is partitioned into three elements: costs related to the fishing activity, the cost of gear, and nonfishing daily operational costs. Finally, FT is an accounting equation that keeps track of time throughout the season. An overview of the fishing process helps solidify an understanding of how this simplified model is expanded into the working model presented in Appendix A.

Fishing process, CPUE – soak time functions, and model calibration

The fishing process involves setting and picking pots, as illustrated in Fig. 1. After soaking a baited pot for 1, 2, or 3 days, the pot is picked from the seabed. Legal male crabs are retained, the pot is rebaited, and the set–pick cycle is repeated for all pots, one at a time, until season closure. This process is common across the fleet, although vessel-specific behavior differs between the two vessel size classes.

Period 1 (P1) consists of the initial setting, picking, and resetting of all pots. The number of pots fished by a small vessel may exceed its carrying capacity, providing that the additional pots are transported to a wet storage area near the fishing ground before the start of the fishing season. Small vessels that choose to fish pots in excess of their vessel carrying capacity take an in-season trip from the fishing grounds to a wet storage area to retrieve additional pots. Small vessels first set all pots initially carried to the grounds before retrieving additional pots. It is assumed that these vessels set all pots that were retrieved from wet storage before starting the picking process, rebaiting and resetting the gear. In period 2 (P2), this pick–set process is repeated for all pots, conceivably numerous times. Anticipation of season closure may require vessels at the end of P2 to reset only a subset of all pots initially fished. It follows that the end of P2 occurs when this subset of pots is reset for final picking in period 3 (P3). Finally, the third and last period consists only of the final pick of all pots fished throughout the season.

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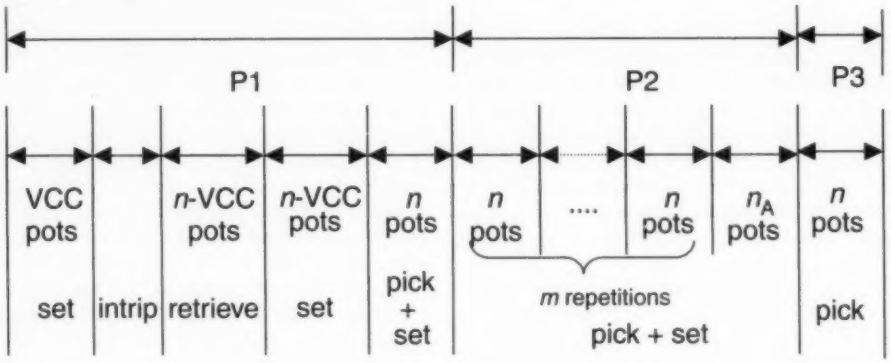
Fig. 1. The fishing process: allocation of time to picking and setting pots. The fishing process involves the setting (set) and picking (pick) of a total of n pots. The time allocated to fishing throughout the season is partitioned into three periods: period 1 (P1), period 2 (P2), and period 3 (P3). During P1, small vessels that choose to fish a number of pots in excess of their vessel carrying capacity (VCC) take an in-season trip (intrip) from the fishing grounds to a wet storage area to retrieve (retrieve) additional pots (n – VCC). In P2, the pick–set process is repeated for all pots, conceivably m times ($m = 0,\ldots,\infty$). Anticipation of season closure may require vessels to reset only a subset n_A of all pots ($0 \leq n_A \leq n$).



The fishing process illustrated (Fig. 1) implies that catch differs across the three periods because soak times differ in each of the three periods. Thus, the variable CATCH in eq. 1 is replaced by P1CATCH, P2CATCH, and P3CATCH. Each of these three periodic catch functions is defined as the year-specific CPUE function evaluated at the period-specific soak time, summed over all pot lifts in the period. For example,

$$\text{(2)} \qquad \text{P1CATCH} = \sum_{i=1}^{n} \beta_0 (1 - e^{(-\beta_2 \text{P1ST}_i)})$$

where i denotes the ith pot, and P1ST_i denotes the first period soak time for pot i. The parameter β_0 represents the year-specific asymptotic catch, and β_2 represents the year-specific rate at which the asymptotic catch is reached.

This analysis simplifies the prior findings of Briand et al. (2001) that the year-specific CPUE function rotates downward throughout the season as the result of stock depletion. Instead, a single average annual CPUE function is assumed to apply throughout a particular season. Year-specific CPUE functions that are representative of evolving fishing conditions throughout the season are chosen through a model calibration process. Model calibration involved adjusting the CPUE function parameters, β_0 and β_2, estimated by Briand et al. (2001), so that year-specific simulations conform to actual fishery harvests and season lengths under historical pot limit policies and historical fishing conditions. The calibrated, year-specific CPUE functions are then used in the analysis of alternative, hypothetical policy scenarios within a given year.

Briand et al. (2001) captured the downward rotation of year-specific CPUE functions by specifying the CPUE parameters, β_0 and β_2, as functions of drop time (DT), i.e., the time at which the pots were placed on the seabed. This detailed specification of the CPUE functions was necessary in the estimation stage of the functions. Proper specification of all factors affecting the level of catch allowed the CPUE – soak time relationship to be verified and avoided estimation biases. Abstracting from this aspect of the CPUE model simplifies the simulation model without affecting its results. Model calibration is accomplished by searching for an appropriate value of DT and corresponding levels of β_0 and β_2 that, when used in the optimization models, produce aggregate year-specific actual catch and season length. The year-specific conditions that prevailed in the 1991–1993 and 1996–1997 Bristol Bay red king crab fisheries, as well as the calibrated CPUE – soak time function parameters, are presented (Table 1).

Optimization

Optimization is achieved when each vessel size adopts the fishing strategy that maximizes quasi-rents subject to the shortest common season length required by the aggregate fleet to harvest the actual, year-specific, fleetwide catch. An individual vessel maximizes quasi-rents by choosing the number of pots fished ($n = 1,\ldots,\text{MaxPots}$), the number of times that pots are soaked throughout the season ($l = 1,\ldots,\infty$), and the number of pots that are reset for the last soak ($n_A = 1,\ldots,(\text{MaxPots} - 1)$). Maximization is assured by complete enumeration of all possible combinations of these three decision variables defining a vessel's optimal behavior. Once optimal individual behavior is determined, fleet behavior is defined by the shortest number of days required to catch the fleetwide harvest.

The process of deriving season length and fleetwide fishery performance from individual vessel behavior is illustrated for a single year. The 1991 optimal fishing behavior of the representative small and large catchers is presented (Table 2). Each individual vessel operator adopts the fishing strategy that maximizes his (her) quasi-rents for the expected season length ranging from 1 to 10 days. Fleetwide catch is the sum of the individual vessel catches. For example, when aggregated across the 302-vessel fleet consisting of 81% small and 19% large vessels in 1991, the fleetwide harvest reached 2.6 millions crabs in a 7-day season (Table 2, bolded row). A 7-day season is the shortest season length required by the aggregate fleet to harvest the actual, year-specific, fleetwide catch under the 1991 fishing conditions embodied in the year-specific CPUE function.

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Table 1. Year-specific model parameters. All catch-per-unit-effort (CPUE) – soak time function parameter values (β_0 and β_2) are based on the work by Briand et al. (2001), calibrated to the year-specific actual fleetwide harvest and fishery season length.

	1991	1992	1993	1996	1997
β_0	14.9	5.5	7	12.7	10.9
β_2	0.7	1.9	2	3.1	3.1
Fleet size	302	281	292	196	256
Small catchers (%)	81	81	71	67	70
Large catchers (%)	19	19	29	33	30
Historic pot limit	None	250	200–250	200–250	100–125
Current pot limit	200–250	100–125	200–250	100–125	100–125
Fleetwide harvest (no. of crabs)	2 630 446	1 196 958	2 261 287	1 249 005	1 315 969
Season length (days)	7	7	9	4	4

Note: Historic pot limit refers to regulations that prevailed in each year. Current pot limit refers to regulations that would apply today in accordance with 5AAC 34.825 (h).

Table 2. Optimal fishing strategy and performance for representative small and large catchers under different expected season lengths.

Expected season length (days)	No. of pots fished	No. of soaks per pot	Soak time per pot (h)	Catch per vessel	Quasi-rents per vessel (US$)
***(a)* Small catcher**					
1	88	2	10.6	488	2 904
2	125	3	17.3	1 456	16 502
3	125	4	19.1	2 364	30 610
4	249	2	37.1	4 146	52 211
5	249	3	39.0	5 542	74 979
6	250	3	40.3	6 949	97 897
7	**250**	**4**	**41.1**	**8 347**	**120 702**
8	250	4	41.7	9 745	143 508
9	250	5	42.2	11 143	166 313
10	250	5	42.6	12 541	189 118
***(b)* Large catcher**					
1	95	2	10.4	534	2 459
2	218	2	22.3	1 951	18 513
3	300	2	32.4	3 748	42 659
4	300	2	36.6	5 370	67 362
5	300	3	39.2	6 989	92 021
6	300	3	40.8	8 598	116 511
7	**300**	**4**	**42.1**	**10 217**	**141 169**
8	300	4	43.0	11 826	165 659
9	300	5	43.7	13 446	190 318
10	300	5	44.2	15 054	214 808

Note: These simulation results are based on the 1991 calibrated catch-per-unit-effort (CPUE) function. Catch is measured in number of crabs caught. The bolded row indicates simulated individual vessels behavior for the 1991 7-day season length. When aggregated across the 1991, 302-vessel fleet (81% small catchers and 19% large catchers), these simulated behaviors yield a total harvest of 2.6 millions crabs, the actual 1991 fleetwide harvest.

The search for individual harvesters' quasi-rent maximizing catch, and the search for the shortest season length that results in an aggregate catch equal to actual fleetwide catch in any given year, were written in the C programming language and run under the Windows 98 operating system. Programming code is available from the authors upon request.

Results and discussion

The results presented in this section address whether or not historic pot limits elongated season lengths and whether catch and quasi-rents were redistributed from large to small catchers. Four different pot limit policies (none, 250 for all vessels, and either 200–250 or 100–125 for small and large vessels, respectively) are examined in the context of the two representative vessel sizes and five different years (1991–1993, 1996–1997). Optimal season length is examined first (Table 3), followed by the optimal levels for each of three variables (number of pots, catch, and quasi-rents) corresponding to the five years and four pot limit scenarios (Table 4). One might think of these tables as a retrospective view of the pot limit policy, as if one were in the 1991 period and contemplating policy options. To assist the reader compare alternative policy scenarios, bolded elements repre-

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Table 3. Simulated year-specific season lengths under alternative pot limits.

	Season length (days)				
Pot limit	1991	1992	1993	1996	1997
None	**7.0**	7.0	8.9	4.0	3.8
Uniform 250	7.1	**7.0**	9.0	4.0	3.8
Two-tiered 200–250	*7.6*	7.0	***9.0***	**4.0**	3.8
Two-tiered 100–125	11.2	*7.8*	10.4	*4.2*	***4.0***

Note: Each column shows the simulated season lengths corresponding to the year-specific catch-per-unit-effort (CPUE) function, actual fleetwide harvest, fleet size, and fleet composition under alternative pot limits. Historic pot limit results are bolded; italicized results reflect current regulations.

sent historical policies and italicized elements represent current policies.

Pot limits do not appear to be effective in elongating seasons (Table 3). Only the most restrictive 100–125 pot limit would have significantly elongated the 1991 season, the one year in which no pot limit existed. Ironically, current regulations would have doubled that pot limit to 200–250 pots, with only a small (0.6 day) season elongation. Similarly, the 1997 pot limit of 100–125 pots, which conforms to current regulations, elongated the 1997 season by just 0.2 days. Even in the one year in which fishery managers were least able to use in-season management to close the fishery, 1996, the most restrictive pot limit would not have been effective. Another irony is apparent in these results. Maximum season elongation, under current regulations, would have occurred in 1992 (0.8 days) and in 1991 (0.6 days). Neither of those years required season elongation for successful in-season management.

These results draw attention to an important generalization. Meaningful season elongation is difficult to achieve in years of poor fishing conditions unless pot limits are even more restrictive. But more restrictive pot limits are unlikely to be politically acceptable. Consider a uniform application of the 100–125 pot limit in all years. Seasons would have elongated just 4.2 days in 1991, 0.8 days in 1992, 1.5 days in 1993, and only 0.2 days in 1996 and 1997. The pot limit is most effective in 1991, which is a year characterized by good fishing conditions (high β_0 and low β_2), large fleet size, and large fleetwide harvest. In contrast, 1996 and 1997 were characterized by bad fishing conditions (low β_0 and high β_2), smaller fleet size, and smaller fleetwide harvest.

The amount of gear, catch, and, finally, quasi-rent that correspond to the optimal season lengths are presented (Table 4). Neither small nor large catcher vessels should necessarily operate with the maximum amount of legal gear (Table 4, "Pots" columns). The optimal strategy for small vessels was to fish approximately half of the legal gear (125 versus 250 pots) in 1992 and (125 versus 200) in 1996, rather than retrieve additional gear from wet storage. Fishing conditions in both years were sufficiently poor so as to render pot retrieval unprofitable. The potential catch per pot (β_0) was particularly small in 1992 and the rate at which a pot reached its potential catch (β_2) was large in 1996. Large vessels would not have fished all allowable gear in 1996, instead voluntarily reducing the number of pots from 250 to 215. This voluntary gear reduction is a consequence of the

Table 4. Simulated year-specific pots fished, catch, and quasi-rents under alternative pot limits, by vessel size.

	1991			1992			1993			1996			1997		
Pot limit	Pots	Catch	Quasi-rents (US$)	Pots	Catch	Quasi-rents (US$)	Pots	Catch	Quasi-rents (US$)	Pots	Catch	Quasi-rents (US$)	Pots	Catch	Quasi-rents (US$)
***(a)* Small catcher**															
None	**250**	**8 347**	**120 702**	125	4038	52 287	217	7327	100 085	125	6027	93 626	125	4896	73 942
250	250	8 507	123 314	**125**	**4047**	**52 419**	214	7369	100 841	125	6027	93 626	125	4896	73 942
200–250	*200*	*8 342*	*121 502*	125	4047	52 419	***200***	***7357***	***101 132***	**125**	**6027**	**93 626**	125	4896	73 942
100–125	100	8 365	121 642	*100*	*4129*	*53 356*	100	7400	106 123	*100*	*6091*	*95 378*	***100***	***4933***	***75 267***
***(b)* Large catcher**															
None	**300**	**10 217**	**141 169**	270	5241	59 098	294	8751	112 164	215	7053	99 163	200	5695	77 559
250	250	9 572	132 208	**250**	**5195**	**59 150**	250	8663	112 411	215.	7053	99 163	200	5695	77 559
200–250	*250*	*10 249*	*142 423*	250	5195	59 150	***250***	***8697***	***112 898***	**215**	**7053**	**99 163**	200	5695	77 559
100–125	125	10 147	137 043	*125*	*4823*	*56 307*	125	8603	113 158	*125*	*6945*	*100 650*	***125***	***5627***	***79 104***

Note: Each column shows the simulated pots fished, individual vessel catch, and individual vessel quasi-rents, corresponding to the year-specific catch-per-unit-effort (CPUE) function, actual fleetwide harvest, fleet size, and fleet composition under alternative pot limits. Historic pot limit results are bolded; italicized results reflect current regulations.

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high rate of catch (β_2); when a pot quickly reaches its potential catch, there is a financial incentive to shorten the soak time, which requires fishing fewer pots.

Finally, note that current regulations would have been binding in all years, restricting both vessel sizes to fish less gear than under the no pot limit scenario. Nevertheless, season length would not have been impacted much by the 100–125 pot limit (Table 3). This observation is especially true in those years when poor fishery conditions would have triggered the most restrictive pot limit because harvesters have an intrinsic economic incentive to adjust fishing behavior to fishery conditions.

Comparison of the alternative scenario outcomes allows one to examine the distributional implications of pot limits relative to the no pot limit policy scenario (Table 4, "Catch" and "Quasi-rent" columns, respectively). Distributive impacts differ between catch and quasi-rents. The actual historical pot limits were essentially distributionally neutral with respect to catch. Large vessels lost 1.2% or less of their potential maximum catch in any year, whereas small vessels gained up to 0.7%. We emphasize, however, that these observations do not suggest that current regulations are distributionally neutral with respect to catch. To illustrate this point, consider 1992.

Weak fishery conditions in 1992 would have invoked the 100–125 pot limit had current regulations been in place. (Note that the 100–125 pot limit yields maximum small-vessel catch and minimum large-vessel catch in every year other than 1991.) Comparing catch under current regulations with the no pot limit scenario reveals that small vessels would have increased catch 2.2% per vessel, whereas large vessels would have lost 8.0% per vessel. This 10.2% differential is related to the previous observations concerning the 1992 CPUE function. Potential catch (β_0) was relatively low in 1992 but the rate at which pots filled (β_2) was at an intermediate level. Small vessels had no economic incentive to retrieve additional gear, but large vessels had an incentive to fish 270 pots. The most restrictive pot limit is more constraining to the large catcher, restricting fishing to only 42% of large vessel carrying capacity. The small vessel, in contrast, could still fish 80% of its carrying capacity. Although the small vessel must give up the opportunity to retrieve more gear, this lost opportunity is offset by a gain in time spent fishing the available pots.

Other interesting nuances concerning the efficiency and distributional impacts of pot limits, as measured by quasi-rents, are apparent. Consider 1997: both small and large vessels benefit financially from the most restrictive pot limit, increasing quasi-rents 1.8% and 2.0%, respectively, over the unrestricted ("none") scenario, a seeming contradiction of nondecreasing ordering constrained versus unconstrained optima. However, optimal behavior under the no pot limit scenario is predicated on the particular fishing strategies that produce the actual 1997 harvest in the simulated season length of 3.8 days. The 100–125 pot limit constrained all vessels, thereby relaxing the season length from 3.8 days to 4.0 days and allowing both vessel size categories to benefit from reduced fishing costs without offsetting redistribution of catch. This modest season elongation is a consequence of bilateral gear reduction, which produced higher quasi-rents compared with the no pot limit scenario. Unilateral reduction in gear would not generate sufficient season elongation to increase both individual and combined quasi-rents. Such a unilateral change in behavior would redistribute catch and quasi-rents to the vessels that do not reduce gear.

The source of potential efficiency gains from industrywide (bilateral) gear reduction is evident by examining how the aggregation restriction on small and large vessels impacts vessel-specific catch and costs. Consider again the 1997 period and the 100–125 pot limit versus no pot limit. Large vessel catch drops 1.2% relative to the no pot limit scenario, whereas large vessel quasi-rent increases 2.0% because of a decline in vessel fishing costs that was greater than the concomitant decline in revenue. The small vessel also benefits from reduced fishing costs, and in addition, it benefits from the redistribution of catch from large to small vessels. Small vessel catch grows 0.7% and its quasi-rent grows 1.8%.

Now suppose instead that the large vessel unilaterally decreases gear to 125 pots, whereas the small vessel fishes its optimal, unrestricted amount of gear, 125 pots. (This unilateral change is not shown in Table 4.) The season elongates only 0.1 days, an insufficient amount of time for cost savings to offset catch and revenue redistribution. Large vessel catch drops 4.2% to 5455 crabs, whereas the small vessel catch increases 2.1% to 4999 crabs. Quasi-rent falls for the large vessel, down 3.3% to US$76 511, whereas small catchers benefit from the redistribution, increasing quasi-rent by 2.3% to US$75 618.

Surprisingly, the current pot limit regulation was not found to reduce efficiency but, rather, modestly enhanced efficiency. Aggregate quasi-rents were computed by multiplying the year-specific fleet composition (Table 1) by the vessel size-specific quasi-rents (Table 4). Fleetwide quasi-rents would have grown 0.7%, 0.6%, 0.9%, 1.7%, and 1.8%, respectively, in each of the five years under the current pot limit regulation relative to the no pot limit scenario.

Not withstanding aggregate efficiency gains, the potential for current pot limit regulations to redistribute wealth from large to small catchers was verified, but only for 1992. Had a 100–125 pot limit been applied in that year, large vessels would have lost 4.7% of their unconstrained quasi-rents, whereas small catchers would have gained 2.0%. Thus, although limited season elongation from pot limits may reduce costs and increase aggregate efficiency, redistribution of catch may leave large vessels financially worse off.

The fact that pot limits were found to redistribute wealth in only a single year and that both vessel sizes would have realized efficiency benefits in all other years raises the question of why large vessels objected strenuously to the pot limit policy. The answer may lie in the assumptions underpinning this study. The analysis assumed that small and large vessels were empowered with knowledge of the actual, year-specific CPUE function. Although the year-specific shape and location of the CPUE function is never known, it is clear that most skippers knew little about the general shape of the CPUE function, especially below two-day soak times. A skipper survey conducted as background information to Briand et al. (2001) revealed that many skippers were astonished that short soak times in 1997 yielded acceptable CPUEs. Before the 100–125 pot limit, the fleet tended to operate under a rule-of-thumb that pots had to soak 2 days to obtain acceptable CPUEs. This revelation caused Briand et

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al. (2001) to speculate that the pot limits may have educated the fleet to the benefits of reduced soak times, even in the absence of pot limits. It also suggests that understanding why large vessels objected to pot limits requires viewing the issue from a perspective of prior behavior–knowledge, i.e., where skippers are assumed to fish the maximum number of pots in 2-day soak rotations, unaware that CPUE does not drop precipitously with shorter soak times.

A catch-maximizing simulation was conducted in which both large and small vessels fished their maximum amount of gear (300 and 250 pots, respectively). When judged against this baseline, redistribution is dramatic. Again consider 1997. The 100–125 pot limit would increase small-vessel quasi-rents 17%, whereas large vessels would lose 3%. Such perceived redistribution would be sufficient for large vessels to fight the pot limit policy. There may be other reasons why large vessels object to pot limits. Additional gear permits grounds preemption–exclusivity. It also enables more efficient prospecting, neither of which were included in this study and both of which can enhance economic performance.

In conclusion, the constrained optimization model presented here captures the basic strategic trade-offs confronting a vessel operator who must decide how to best allocate time over a given season. It demonstrates that the pot limit policy is premised on a naïve conception of fishing power that is equated with the amount of gear fished per vessel. A blanket statement that less gear elongates the season sufficiently to improve in-season management does not account for the fact that fishing power is also a function of fishing conditions. Nor does it account for the intrinsic economic incentives that vessels have to adjust fishing strategies to those year-specific fishing conditions. Current regulations fail to include these dimensions of fishing power.

There is no evidence that pot limits elongated the season sufficiently to improve in-season management — the policy goal. In the years when stock status and fleet size would have dictated a 100–125 pot limit under current regulations, e.g., 1992, 1996, and 1997, meaningful season elongation was not forthcoming. Pot limits effectively elongate season only when relatively strong fishing conditions make season elongation unnecessary for in-season management, e.g., 1991 and 1993. In fact, economic incentives appear to be sufficient impetus for vessels to reduce gear voluntarily during years when seasons are short, i.e., in years characterized by low GHL, large fleet size, and less favorable fishing conditions, including both low and high potential CPUE (small β_0) and rapid fill rate (large β_2). A pot limit policy based on stock status and fleet size does not consider intrinsic economic incentives to adjust fishing behavior to fishing conditions.

Surprisingly, the current pot limit policy was found to improve efficiency. It elongates the season, if only slightly, but allows vessels to capture efficiency gains that arise from industrywide reduction in fishing capacity. Though unintended redistributional consequences would seem inevitable, pot limits were found to redistribute wealth in only a single year of the five years examined. Both vessel size classes benefited from mutual gear reduction in all but 1992. Economic incentives alone, however, cannot be relied upon to promote voluntary gear reduction. Left to individual quasi-rent maximizing incentives, gear will not be reduced sufficiently to yield efficiency gains that depend on industrywide reduction. The fact that industrywide gear reduction is legally permitted under cooperative behavior but is not part of the fabric of this fishery suggests transaction and enforcement costs exceed any efficiency gains from fleetwide cooperation. The use of additional gear for the purpose of grounds preemption–exclusivity and prospecting further inhibit voluntary gear reduction.

Finally, it is important to point out that the results of this paper are based on a deterministic model of a process that is inherently stochastic from year to year, as well as across individual fishing vessels within years. The present analysis of pot limit policies spans a number of years during which there was considerable variation in fishing conditions, thus providing some insight into the variation in policy impacts that can be caused by changing fishing conditions over time. However, future research is needed to collect the detailed data necessary to estimate a distribution of fishery productivity over vessels and, over time, to provide a more complete assessment of the policy impacts on individual fisherman.

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Appendix A. Full model specification

The harvester's constrained optimization problem is presented in eqs. A1–A15.

$$\text{(A1)}\quad \text{MaxQR} = p(1-\alpha)(\text{P1CATCH} + \text{P2CATCH}(1 - I_{\{1,2\}}(l)) + \text{P3CATCH}(1 - I_{\{1\}}(l))) - \text{FISHINGcost} - \text{POTcost} - \text{DAILYcost}$$

subject to $\text{FT} \leq \text{SL}_{\text{EXP}}$ and $n \leq \min[\text{PotLimit}, \text{MaxPots}]$, where QR denotes quasi-rents (revenue in excess of variable costs) retained by the vessel; p denotes the exvessel price of crab, α denotes the crew share, and P1CATCH, P2CATCH, and P3CATCH are vessel catches of periods 1, 2, and 3, respectively; l is the number of times that pots are soaked throughout the season; and $I_{\{\}}(l)$ is an indicator function that equals one when l is contained in the specified interval, zero otherwise. This indicator function is used to allow for the possibility of only a single soak during the season or for only two soaks; conceptually, it could be optimal for a vessel operator to fish so many pots that each would be soaked only once or twice during the whole season. If pots are soaked only once, only period 1 is modeled. If pots are soaked only twice, only periods 1 and 3 are modeled. The first term in the objective function is gross revenue to the vessel, net of crew share. The other terms are the variable fishing costs, which fall into three categories: (1) FISHINGcost, which varies with the fishing intensity, (2) POTcost, which varies with the number of pots fished, and (3) DAILYcost, which depends on the number of days that a vessel operates (FT). SL_{EXP} denotes the operator's preseason expectation of season length. The number of pots (n) that the operator fishes cannot exceed the lesser of the vessel size specific pot limit (PotLimit) or the maximum number of pots that a vessel may fish (MaxPots). A large catcher is assumed to fish at most its vessel carrying capacity of 300 pots, whereas a small catcher is assumed to fish a maximum of 250 pots, twice its vessel carrying capacity made possible by the use of wet storage of 125 pots.

Each of the three periodic catch functions is defined as the year-specific CPUE function evaluated at the period-specific soak time, summed over all pot lifts in the period.

$$\text{(A2)}\quad \text{P1CATCH} = \sum_{i=1}^{n} \beta_0(1 - e^{-\beta_2 \text{P1ST}_i})$$

$$\text{(A3)}\quad \text{P2CATCH} = m\sum_{i=1}^{n} \beta_0(1 - e^{-\beta_2 \text{P2ST}}) + \sum_{i=1}^{n_A} \beta_0(1 - e^{-\beta_2 \text{P2ST}})$$

$$\text{(A4)}\quad \text{P3CATCH} = \sum_{i=1}^{n} \beta_0(1 - e^{-\beta_2 \text{P3ST}_i})$$

where i denotes the ith pot. The parameter β_0 represents the year-specific asymptotic catch, and β_2 represents the year-specific rate at which the asymptotic catch is reached. CPUE differs across the three fishing periods because each is characterized by a different soak time. The initial period soak time (P1ST_i) differs from the midseason soak time (P2ST) and the final soak time (P3ST_i). The first- and third-period terms are subscripted to reflect soak times that differ from pot to pot, whereas the second-period soak times are constant across all pots by definition and thus carry no subscript.

Consider soak time in period 1. The soak time for the first pot set is determined by the amount of time that it takes to set all remaining pots in the initial period, including any time spent obtaining additional gear from wet storage. The initial soak time for the last pot is determined by the amount of time that it takes to pick and reset all prior pots. The initial soak time of any other pot is determined by its exact position in the fishing sequence. The soak time accounting protocol is given in eq. A5.

$$\text{(A5)}\quad \text{P1ST}_i = (n - i)\text{SET} + (i - 1)(\text{PICK} + \text{SET}) + \{\text{INTRIP} + (n - \text{VCC})\text{RETRIEVE}\}I_{\{[1,\text{VCC}],(\text{VCC},2\text{VCC}]\}}(i,n)$$

where $I_{\{[1,\text{VCC}],(\text{VCC},2\text{VCC}]\}}(i,n)$ is an indicator function that captures the effect of obtaining additional gear from wet storage on pot i soak time. This zero–one indicator equals one when the number of pots fished exceeds VCC and the ith pot is in the closed interval [1,VCC]. When either of these two conditions is not met, the indicator function equals zero.

Soak times in period 2 are characterized by set–pick repetitions of all gear, which are now fully established and of equal duration, i.e., all pots have identical soak times throughout period 2.

$$\text{(A6)}\quad \text{P2ST} = (n - 1)(\text{PICK} + \text{SET})$$

The fishing season ends in period 3. Two features distinguish the soak times in this period. First, pre-announced season closure may eclipse the terminal period such that not all n pots are reset at the end of period 2. Second, the subset of pots set at the end of period 2 is picked in period 3 but not reset. The pots not reset at the end of period 2 are also picked in period 3. As in period 1, the soak time of any pot is determined by its exact position in the fishing sequence. Note that the time spent stacking pots in this period is assumed negligible in determining soak times.

$$\text{(A7)}\quad \text{P3ST}_i = (n - 1)\text{PICK} + (n_A - i)\text{SET} + n(\text{SET})I_{(n_A,n]}(i)$$

where $I_{(n_A,n]}(i)$ is an indicator function that captures the fact that a subset of pots, n_A, are reset one additional time at the end of period 2. The zero–one indicator equals one when i is between n_A and n and is zero otherwise.

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FISHINGcost includes fuel and bait costs. POTcost includes pot registration costs, costs due to pot loss, pot maintenance costs, and costs incurred by fishing a number of pots in excess of the vessel carrying capacity. DAILYcost includes food and daily pro rata maintenance expense, both of which are a function of FT.

$$\text{(A8)}\quad \text{FISHINGcost} = (n(m+2)+n_A)[(\text{PICK}+\text{SET})\cdot\text{FUELFISH}\cdot\text{FUELPRICE}+\text{BAITPRICE}]$$

$$\text{(A9)}\quad \text{POTCOST} = n(\text{REGIST}+\text{pctLOSS}\cdot\text{POTPRICE}+\text{pctMAINT}\cdot\text{IMAINT}) + \begin{Bmatrix}(\text{PRETRIP}+\text{INTRIP}+\text{POSTRIP})\cdot\text{FUELRUN}\cdot\text{FUELPRICE}\\ +(\text{PRETRIP}+\text{POSTRIP})(\text{DMAINT}+\text{DFOOD})\\ +(n-\text{VCC})\cdot\text{RETRIEVE}\cdot\text{FUELFISH}\cdot\text{FUELPRICE}\end{Bmatrix} I_{(\text{VCC},2\text{VCC})}(n)$$

$$\text{(A10)}\quad \text{DAILYcost} = \text{FT}(\text{DMAINT}+\text{DFOOD})$$

$$\text{(A11)}\quad \text{FT} = (n(m+2)+n_A)(\text{PICK}+\text{SET})+\{\text{INTRIP}+(n-\text{VCC})\text{RETRIEVE}\}I_{(\text{VCC},2\text{VCC})}(n)$$

where $I_{(\text{VCC},2\text{VCC})}(n)$ is an indicator function that takes on the value one when the value of n is between VCC and 2VCC and equals zero otherwise. Terms attached to the indicator function pertain only to the small vessel, which may fish a number of pots up to twice its vessel carrying capacity. All variable definitions are given in Table A1.

Table A1. Quasi-rent function parameters include (*a*) revenue function parameters, (*b*) variable cost function parameters, and (*c*) constraints parameters.

		Small catcher	Large catcher
(*a*) Revenue function parameters			
α	Crew share	29%	33%
p	Exvessel price of crab	\$25·crab^{-1}	\$25·crab^{-1}
SET	Individual pot bait set time	2.4 min	2.4 min
PICK	Individual pot retrieval harvest time	8.6 min	7.5 min
INTRIP	Time spent on one in-season trip to storage	10 h	10 h
RETRIEVE	Individual pot retrieval time at storage area	3 min	3 min
VCC	Vessel's pot carrying capacity	125 pots	300 pots
β_0	Asymptotic catch of CPUE function		
β_2	Rate at which β_0 is reached		
(*b*) Variable cost function parameters			
FUELPRICE	Price of fuel per gallon	\$1·gal^{-1}	\$1·gal^{-1}
PRETRIP	Time spent on one preseason trip to storage	40 h	40 h
POSTRIP	Time spent on one trip back to grounds	30 h	30 h
FUELRUN	Fuel consumption while running	30 gal·h^{-1}	40 gal·h^{-1}
FUELFISH	Fuel consumption while fishing	25 gal·h^{-1}	30 gal·h^{-1}
BAITPRICE	Price of bait per pot for each soak	\$7.50·pot^{-1}	\$7.50·pot^{-1}
DMAINT	Daily maintenance costs	\$300·day^{-1}	\$500·day^{-1}
DFOOD	Daily food costs	\$130·day^{-1}	\$150·day^{-1}
REGIST	Registration cost per pot	\$2.50·pot^{-1}	\$2.50·pot^{-1}
pctLOSS	Percentage of lost pots	1%	1%
POTPRICE	Price per pot	\$1000·pot^{-1}	\$1000·pot^{-1}
pctMAINT	Percentage of pots reworked	30%	30%
IMAINT	Maintenance cost per pot	\$100·pot^{-1}	\$100·pot^{-1}
(*c*) Constraints			
MaxPots	Maximum number of pots with which the vessel may fish	250	300

Note: All parameter values for the catch-per-unit-effort (CPUE) function are year-specific, calibrated such that year-specific simulation results conform to actual fishery harvests and season lengths (see the section Fishing process, CPUE – soak time functions, and model calibration). Currency is expressed in US dollars throughout.

The above specification of the period-specific soak time and variable cost functions assumed that the fishing process consists of least three periods. Again, completeness requires allowing for the possibility of only a single soak during the season or for two soaks, $l \geq 1$. This additional flexibility is achieved by incorporating indicator functions dependent on l into a number of the soak time and cost components of the model, as shown below.

$$\text{(A12)}\quad \text{PIST}_i = \begin{Bmatrix}(n-i)\text{SET}+(i-1)(\text{PICK}+(1-I_{\{1\}}(l))\text{SET})\\ +\{\text{INTRIP}+(n-\text{VCC})\text{RETRIEVE}\}I_{\{(\text{VCC},2\text{VCC}]\cup[1,\text{VCC}]\}}\end{Bmatrix}(n,i)\Big\}(1-I_{\{(n_A,n],\{2\}\}}(i,l))$$

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$$\text{(A13)}\quad \text{P3ST}_i = (n_\text{A} - i)\text{SET} + n(\text{SET})I_{(n_\text{A},n]}(i) + (n-1)\text{PICK}(1 - I_{[(n_\text{A},n],\{2\}]}(i,l)) + (i-1)(\text{PICK})I_{[(n_\text{A},n],\{2\}]}(i,l) + \{\text{INTRIP} + (n - \text{VCC})\text{RETRIEVE}\}I_{[(n_\text{A},\text{VCC}],(\text{VCC},2\text{VCC}],\{2\}]}(i,n,l)$$

$$\text{(A14)}\quad \text{FISHINGcost} = \{n + n_\text{A}I_{(2,\infty]}(l) + (n(1+m))I_{[3,\infty)}(l)\} \times [(\text{PICK} + \text{SET})\cdot\text{FUELFISH}\cdot\text{FUELPRICE} + \text{BAITPRICE}]$$

$$\text{(A15)}\quad \text{FT} = \{n + n_\text{A}I_{[2,\infty)}(l) + (n(1+m))I_{[3,\infty)}(l)\}(\text{PICK} + \text{SET}) + [\text{INTRIP} + (n - \text{VCC})\text{RETRIEVE}]I_{(\text{VCC},2\text{VCC}]}(n)$$

Parameterization of the full model specification for a representative small and large catcher is found in Table A1. Cost and fishing practices information were gathered originally by Lynch (1997) and updated by way of personal communication with vessel operators.

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Seasonal and ontogenetic patterns in the migration of anadromous brook charr (*Salvelinus fontinalis*)

Sophie Lenormand, Julian J. Dodson, and Annie Ménard

Abstract: Migration patterns of brook charr (*Salvelinus fontinalis*) from the Sainte-Marguerite River, Québec, Canada, were investigated to explore the hypothesis that migratory behaviour changes according to size during the critical period of first downstream migration, when survival is likely to be related to size, and during subsequent seasonal movements. We hypothesized that as fish grow, they should adopt more conservative behaviours to protect the reproductive assets that they have accumulated. First downstream migration occurred over a month in spring. Larger juvenile charr migrated early, whereas smaller charr seemed to delay offshore migration. As predicted, migratory patterns of charr changed through ontogeny. Sea age 0 juveniles stayed in estuarine areas until October and overwintered outside their natal river. Sea age 1 juveniles returned to their natal river earlier in the fall and some of them overwintered there. Adults (some sea age 1 migrants and older migrants) undertook their upstream migration to spawning areas from July to September, larger ones migrating earlier than smaller ones. Postspawners migrated downstream after reproduction or overwintered in the river. Environmental differences related to geographical location may be responsible for the variation of migration patterns and other life-history traits observed among brook charr populations, emphasizing the coevolution of anadromy and life history.

Résumé : Les patrons de migration de l'omble de fontaine (*Salvelinus fontinalis*) de la rivière Sainte-Marguerite, Québec, Canada, ont été étudiés dans le but d'explorer l'hypothèse selon laquelle le comportement migrateur change en fonction de la taille lors de la période critique de la première dévalaison, où la survie est susceptible de dépendre de la taille, mais aussi lors des mouvements saisonniers ultérieurs car, au fur et à mesure que les poissons grandissent, ils devraient adopter des comportements de plus en plus prudents pour protéger les atouts reproductifs qu'ils ont accumulés. La première dévalaison se déroulait sur un mois, au printemps, mais les migrants les plus grands descendaient la rivière en premier tandis que les plus petits semblaient retarder leur migration vers le large. Tel que prédit, les patrons de migration des ombles changeaient au cours de leur ontogénie. Les juvéniles d'âge en mer 0 restaient en estuaire jusqu'en octobre et passaient l'hiver hors de leur rivière natale. Les juvéniles d'âge en mer 1 regagnaient leur rivière natale plus tôt à l'automne et une partie d'entre eux passaient l'hiver là. Les adultes (une partie des migrants d'âge en mer 1 et les migrants d'âge en mer supérieur) entreprenaient leur migration vers les sites de fraie de juillet à septembre, les plus grands plus tôt que les plus petits. Les géniteurs dévalaient à nouveau après la reproduction ou passaient l'hiver en rivière. Les différences environnementales associées à la situation géographique peuvent expliquer les variations des patrons de migrations et du cycle vital qui sont observées entre les populations d'ombles de fontaine, mettant en évidence l'évolution conjointe du comportement anadrome et du cycle vital.

Introduction

Migration involves specialized behaviours that have arisen through natural selection (Dingle 1980). Therefore, migrants are expected to maximize their inclusive fitness by changing habitats when appropriate (Krebs and Davis 1993). From this evolutionary perspective, Gross (1987) developed a model for understanding diadromy: fish would migrate if "the growth and survivorship advantages of utilizing a second habitat, plus the cost of moving between habitats ... exceed the advantages of staying in only one habitat for the same period of time". Concerning anadromy in salmonids, though moving to salt water involves energetic costs, osmotic stress, and a higher predation risk than in fresh water, the fitness payoff of migration to sea results from an enhanced growth rate in a richer feeding area (Jonsson and Jonsson 1993).

Salmons (*Oncorhynchus gorbuscha*, *O. keta*, *O. kisutch*, *O. masou*, *O. nerka*, *O. tshawytscha*, and *Salmo salar*) undertake only two transitions between fresh and salt water before reproduction: one at smolting and the other when mature individuals return to reproduce. However, in many charr

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(*Salvelinus*) and trout (e.g., *Oncorhynchus clarki*, *Salmo trutta*) populations, fish move back and forth between their natal rivers and estuarine areas at the juvenile and adult stages (Randall et al. 1987). As in salmon, some of their movements are clearly ontogenetic in nature. There is first a downstream migration, the timing of which depends on size and growth rate (e.g., Økland et al. 1993; Rikardsen et al. 1997; Thériault and Dodson 2003), and then an upstream migration to spawning areas. Other movements are related to seasonal changes affecting the habitats exploited. Juveniles and adults tend notably to overwinter in fresh water (Randall et al. 1987). According to the model of Gross (1987), such observations imply that the growth–mortality trade-off constraining anadromy varies among seasons.

The immediate advantages and costs of staying in a given habitat may vary with the individual's body size (Werner and Gilliam 1984). In salmonids, where osmotic stress is lower for larger migrants (McCormick and Saunders 1987) and vulnerability to predation and disease may also decrease with greater size (Marschall et al. 1998), a common example of size-dependent costs of migration to sea is size-selective mortality during or shortly after migration to sea (references in Bohlin et al. 1996). Moreover, even in the absence of size-dependent effects on growth or mortality, dynamic models suggest that lifetime fitness benefits of any behavioural act may depend on the individual's age, size, or physiological state at the time that the act is performed (McNamara and Houston 1986; Ludwig and Rowe 1990; Clark 1994). Individuals with greater reproductive value (e.g., juveniles close to size at maturity, adults with a large size and in good condition) should be more averse to risk predation because they would gain less from a given absolute increase in reproductive assets relative to what they would lose if caught by a predator (Clark 1994). Therefore, we would expect that the migratory behaviour of salmonids carrying out seasonal movements would change according to the individual's age (or age since migration, if size depends more on sea age than on total age), maturity stage, size, and condition.

Although this issue has never been studied as such, there is some evidence that seasonal migrations differ according to the individual's size in several charr and trout populations. For instance, larger individuals return to fresh water sooner than smaller ones (e.g., Castonguay et al. 1982; Dempson and Green 1985; Jonsson 1985). Castonguay et al. (1982) also suggested that smaller brook charr (*Salvelinus fontinalis*), corresponding to migrants-of-the-year, do not return to the Saint-Jean River, Québec, at the end of the summer growing season. If such size- or age-dependent patterns exist, their study is of major importance for the protection and enhancement of salmonid populations. First, the identification of how different life stages may be exposed to different rates of exploitation in time and space is an obvious prerequisite to the establishment of successful local management plans. Moreover, the effectiveness of conservation policies relies on a good understanding of the evolution of salmonid life history, which is intimately connected with anadromy. Migratory behaviour and other life-history traits should co-evolve to form adaptive strategies that convey selective advantages in specific environmental settings (Hutchings and Morris 1985). Ontogenetic patterns in the migration of salmonid populations would represent optimal behavioural paths towards the maximization of inclusive fitness and may provide interesting insights into the evolution of anadromy.

The brook charr is native to eastern North America, where it is one of the most popular game fishes. Like many salmonids, it may exist as migratory and freshwater resident forms that differ in life-history patterns (Power 1980). Marine movements of anadromous brook charr are of short duration (2–4 months) and seem to be limited to estuarine and coastal regions near their natal river (e.g., Castonguay et al. 1982; O'Connell 1982; Montgomery et al. 1990). Reproduction takes place in the fall, but adults start their upstream migration during the summer. Anadromous brook charr usually mature during their second or third growing season in salt water and multiple spawning is common (Power 1980). There are, however, significant differences between populations. Ages at first downstream migration range from 1 to 7 years (Randall et al. 1987). Although exploitation of estuarine areas usually takes place during the summer, a variety of seasonal movements has been described throughout the *S. fontinalis* distributional range (reviewed by O'Connell 1982; LeJeune 1987). The extensive life-history and behavioural differences observed in brook charr makes this species a particularly interesting model in which to explore the relationship between anadromous behaviour and the evolution of life history (see Dodson 1997).

In the present study, we explored the hypothesis that migratory behaviour of anadromous brook charr changes according to their size during the critical period of first downstream migration (when survival is likely to be related to size) but also during subsequent seasonal movements, as larger fish should be more averse to risk to protect the reproductive assets that they have accumulated. Migratory patterns were investigated combining a monitoring of first downstream migration, direct sampling in estuarine areas, creel census, and a mark–recapture experiment, in collaboration with anglers. Seasonal movements were analyzed according to sea age, maturity stage, and size of individuals. We predicted that as fish grow, they should opt for more conservative migratory behaviours.

Materials and methods

Study area

The Sainte-Marguerite River (48°27′N, 69°95′W; Fig. 1) empties into the Saguenay Fjord, 25 km upstream from its confluence with the St. Lawrence maritime estuary (Québec, Canada). It is divided in two main branches: the Principal Branch and the Northeast Branch, each of which is 100 km long and around 25 m wide and drains an area of 1000 km^2. Daily flows range between 10 m^3·s^{-1} (February) and 430 m^3·s^{-1} (May). The river is ice-covered from December to April. Maximum observed water temperature during the study was 25 °C (July). In addition to brook charr, the river also contains Atlantic salmon (*Salmo salar*) and, to a lesser extent, longnose and white sucker (*Catastomus catastomus* and *C. commersoni*), longnose dace (*Rhinichthys cataractae*), fallfish (*Semolitus corporalis*), and American eel (*Anguilla rostrata*). Predators of anadromous charr present in the river are merganser (*Mergus merganser*), mink (*Mustela vison*), osprey (*Pandion haliaetius*), and river otter (*Lutra canadiensis*).

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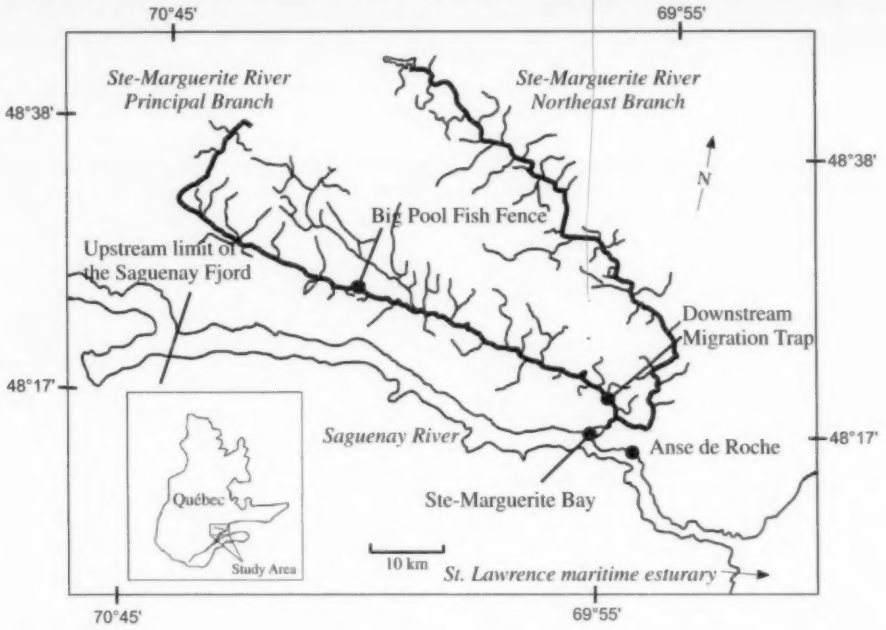
Fig. 1. Location of the Sainte-Marguerite River – Saguenay River system and sampling sites in the province of Québec, Canada.



Anadromous charr migrate to the Sainte-Marguerite River estuary, which forms a large shallow bay, the Sainte Marguerite Bay. From there, they have access to the Saguenay River (Fig. 1). The 100-km downstream part of the Saguenay River (the Saguenay Fjord), under tidal influence, is a mixing zone between fresh water coming from upstream and salt water coming from the St. Lawrence maritime estuary. In a subarctic fjord such as the Saguenay, freshwater inputs are considerable and show important fluctuations. From May to October, strong thermohaline stratification is observed. The water column is divided into a thin mixed layer (5–10 m) of warm (5–15 °C), brackish (0–18‰) water and a thick (up to 275 m), underlying layer of cold and saline water (<0.5 °C, >26‰ at 15 m). In the fall, as surface temperature decreases, exchanges between the two layers increase and salinity at the surface rises to 22‰ in November. During the ice-covered period (December to April), surface temperature stays around 0 °C and surface salinity stabilizes at low values (less than 7‰ vs. 20‰ at 10 m). From mid-March to the beginning of May (ice-melt period), the increase of freshwater inputs and surface water temperature gradually restores the summertime thermohaline stratification (Chassé and Côté (1991) and references therein).

The Saguenay River is characterized by a low primary production but high densities of zooplankton. At least 410 species of marine benthic invertebrates are present in the fjord (ZIP Saguenay 1998). Among them, amphipods (Gammaridae), mysids, and polychaetes may constitute major prey items for juvenile anadromous brook charr, as observed in other estuaries (White 1940; Gaudreault et al. 1982). Fish populations are also relatively diverse, with 76 species recorded to date. Common prey of large (more than 25 cm) anadromous charr are present: smelt (*Osmerus mordax*), sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*), and sand lance (*Ammodytes* spp.). High productivity and abundance of large prey (large invertebrates and fish) are two factors that may explain the fast growth of salmonids in the sea vs. in river systems (Keeley and Grant 2001). Thus, as in many estuaries, the Saguenay River should constitute a better feeding habitat than charrs' natal river, especially in winter when prey are still abundant in the former area. However, predation risk is also likely to be higher in the Saguenay River. Potential predators of anadromous charr in that area are cormorant (*Phalacrocorax auritus*), heron (*Ardea herodias*), loon (*Gavia immer*), merganser (*Mergus merganser*), osprey (*Pandion haliaetius*), harbor seal (*Phoca vitulina*), and Greenland shark (*Somniosus microcephalus*).

Sampling and mark–recapture experiment

Anadromous brook trout were sampled and tagged at different life stages during 4 years (1998–2001). In 1999 and 2000, descending charr were caught by an Alaskan trap (1-cm mesh) set 7 km from the river's mouth on the Principal Branch of the Sainte-Marguerite River (Fig. 1). Monitoring started just after the ice breakup period, when discharge was beginning to decrease, and ended when catches had been minor for 10 consecutive days. The trap covered one-third of the river and caught at least 1000 charr every year. Fish were measured (fork length (FL), to the nearest mm). Twelve percent of total catches in 1999 and 10% in 2000 were sacrificed for laboratory analyses (see below). The rest of the fish were marked with clear, individually labelled T-bar anchor tags (Floy FF-94), provided that their fork length was greater than 75 mm. Tag retention was tested in an aquarium with 20 fish ranging in size from 75 to 132 mm FL. No tag loss, mortality, or serious injury was observed after 3 months.

In the Sainte-Marguerite Bay, sampling and tagging of anadromous juveniles was carried out by approximately weekly hauls of a 40-m beach seine (0.5-cm mesh, 1.5 m

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deep) in September and October 1998, from the beginning of May until mid-October in 1999 and 2000, and in May 2001. All fish caught by seining were measured; recaptures were recorded and untagged fish were marked with T-bar tags (Floy FF-94). In July 1999, we made two additional seine samplings in a deeper, colder, and more saline area of the Saguenay Fjord, Anse de Roche (Fig. 1), where several migrants-of-the-year had been recaptured by anglers. Every year, anadromous spawners were sampled during their upstream migration by inserting a trap into the Big Pool (Fig. 1) fish fence (wire covered by a net, 4-cm mesh). The fence only operates in July and serves to delay the upstream migration of Atlantic salmon for conservation purposes. An additional seine haul (5-cm mesh) was made at the same location at the end of August to complete the sampling. All fish were measured and those that were not recaptures were tagged with T-bar tags (Floy FD-94).

Fishing for anadromous charr is permitted in the Saguenay River (including Sainte-Marguerite Bay) all year long and in the Sainte-Marguerite River from 15 June to 31 October. Tag returns from the sportfishery were encouraged with a $5 cash reward and the opportunity to participate in an annual draw for prizes. In 1998, 1999, and 2000, we completed the mark–recapture experiment by a creel census in the Sainte-Marguerite River and the Sainte-Marguerite Bay. Two registration stations were operated, at 30 km upstream on the river and at the river's mouth. Catches were measured and weighed. In the fall, future spawners or postspawners were identified according to external signs of maturation (hooknose, orange to black belly, and sperm outflow by abdominal stripping in males; dilation of urogenital papilla and egg outflow by abdominal stripping in females). Subsamples of fish were dissected for more detailed analysis (see below) on a regular basis.

In winter, as angling is forbidden in the Sainte-Marguerite River, we made two additional samplings under ice cover, using four rods baited with worms and corn: in the downstream pools of the Sainte-Marguerite on 20 February 2000 and 31 January 2001 and at the river mouth on 1 and 16 February 2001. All fish caught were sacrificed for laboratory analysis.

Charr that had been sacrificed or sampled from anglers (tagged fish and subsamples of untagged fish) were measured, weighed, and classified with respect to sex and stage of maturity (Nikolskii 1963). Stomach contents were analysed for a related study (conducted by Geneviève Morinville and Joe Rasmussen, Department of Biology, McGill University, Montréal, QC H3A 1B1, Canada). Sagittal otoliths were removed, cleaned, and fastened to glass slides with a clear mounting adhesive at its melting point (50 °C). After hardening of the adhesive, total age and age at downstream migration were read under a binocular microscope using reflected light. Age at downstream migration was determined at the first major increase of annulus width (Fig. 2). This method was tested using fish that had been tagged during their downstream migration (i.e., fish for which sea age was already known) and were subsequently recaptured after several years in salt water. The sea age of 95% of 545 tagged fish (528) was correctly identified based on otolith microstructure. As a result, total age and age at sea of all sacrificed fish were identified using otoliths.

Data analysis

First downstream migration was characterized according to age and body size of migrating charr. Seasonal migratory patterns were analyzed according to sea age, maturity stage, and body size of migrants. Differences in length between two groups were tested by two-tailed Student's t test when data met the required assumptions and by Mann–Whitney U test otherwise. Total length distributions (all charr caught) were right-skewed in both years and differed significantly from normal distributions. However, for a given age class, lengths were normally distributed and samples met the required assumptions to be compared by Student's t tests. Proportions were compared by χ^2 test (using Yates' correction for continuity when some expected frequencies became less than 10). Statistical analyses were performed using Statistica 5.5.

Results

First downstream migration

The monitoring of downstream migration in 1999 and 2000 resulted in the capture of 1483 and 1019 migrants-of-the-year, respectively. Subsamples of 178 fish in 1999 and 92 in 2000 were used for age determination. According to the temporal distributions of catches in the trap (Fig. 3), we probably missed the onset of downstream migration in 1999. However, the first significant catches of first-time migrants in Sainte-Marguerite Bay (SMB) started 4 days after the trap was installed in the river and included recaptures of fish tagged in the trap. Therefore, the migration peak that we observed on the first day of monitoring was most likely the first one. In both years, the outmigration of brook charr occurred over a period of approximately 1 month (Fig. 3). Migration time (days after first day of monitoring) decreased with length of migrating charr (1999, slope = –0.116, R^2 = 0.07, $p < 0.0001$; 2000, slope = –0.083, R^2 = 0.05, $p < 0.0001$). Although significant, the relationships are weak as the migration of smaller fish was distributed throughout the period of outmigration, whereas larger fish were observed mostly at the beginning of the outmigration (in 1999, 50% of fish of FL < 120 mm had not migrated before day 10, whereas 70% of fish of FL ≥ 120 mm had migrated by day 9, and in 2000, 50% of fish of FL < 120 mm had not migrated before day 15, whereas 72% of fish of FL ≥ 120 mm had migrated by day 14).

There was no significant difference in the length of emigrating charr between 1999 and 2000 samplings (Fig. 4): 1999, mean FL = 111.8 mm; 2000, mean FL = 112.4 mm; Mann–Whitney U test, $z = -1.19$, $p = 0.23$. Charr belonged to three age classes: 1+ (29% of migrants in 1999 and 26% in 2000), 2+ (68% of migrants in 1999 and 69% in 2000), and exceptionally 3+. Fish migrating at age 2 were significantly bigger than fish migrating at age 1 (1999, 2+ FL ± standard deviation (SD) = 118.4 ± 14.7 mm and 1+ FL = 89.0 ± 9.8 mm, $t = -14.8$, $p < 0.001$; 2000, 2+ FL = 114.5 ± 16.2 mm and 1+ FL = 91.0 ± 10.8 mm, $t = -7,33$, $p < 0.0001$). None of the sampled fish showed any signs of a previous reproduction.

When they entered the SMB, migrants-of-the-year (sea age 0 migrants) were easily distinguished from migrants of greater sea age because of almost no overlap between length

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Fig. 2. Left sagittal otolith of age-3 brook charr (*Salvelinus fontinalis*) caught in the Sainte-Marguerite River (Big Pool, July 2000) with different migratory patterns: (*a*) charr having migrated at age 1, (*b*) charr having migrated at age 2, and (*c*) freshwater resident charr. Downstream migration is characterized by a major increase of annulus width. Numbers in italics indicate beginning of year *n*. Otoliths in (*b*) and (*c*) were enlarged relative to otolith in (*a*) to enhance comparisons.

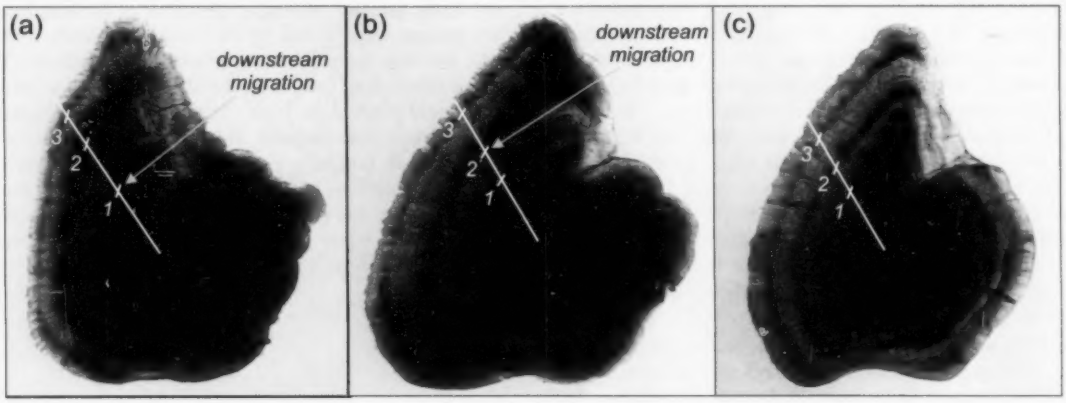


Fig. 3. Number of emigrating brook charr (*Salvelinus fontinalis*) caught per day in the Principal Branch trap in 1999 (solid line) and 2000 (broken line).

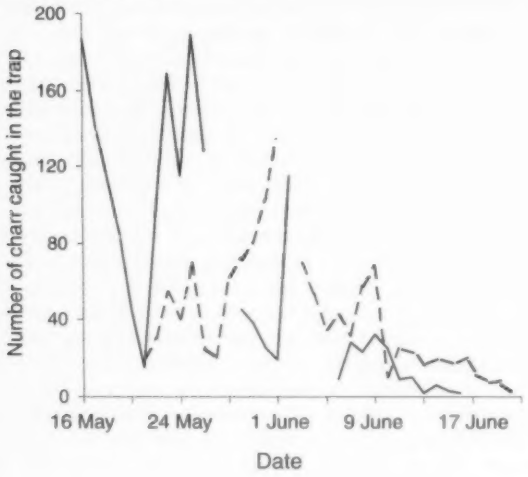
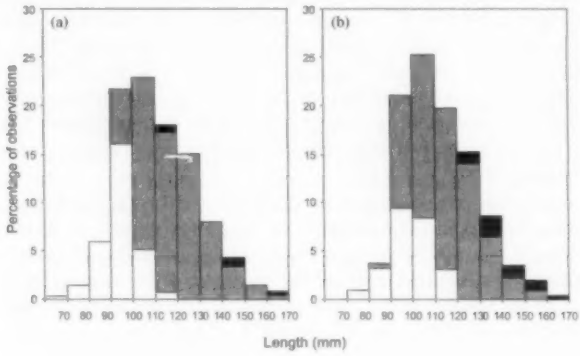


Fig. 4. Length frequencies of all emigrating brook charr (*Salvelinus fontinalis*) caught in the Principal Branch trap from mid-May to mid-June in (*a*) 1999, n = 1483, and (*b*) 2000, n = 1019, and distribution of ages (1+, open bars; 2+, shaded bars; 3+, solid bars) in length classes according to laboratory analysis (1999, n = 178, and 2000, n = 92).



distributions of sea age 0 and sea age 1 charr: by the third week of May 1999 and 2000, more than 97% of sea age 1 charr (charr having migrated in the spring of 1998 and 1999, respectively) had a fork length greater than 155 mm (seine sampling: 1999, n = 43; 2000, n = 49), whereas more than 99% of new migrants had a fork length smaller than 155 mm.

The tagging program

A total of 8412 charr were marked with T-bar tags from September 1998 until August 2001. We recaptured 1262 (15.0%) of these fish during subsequent samplings. Anglers from the Sainte-Marguerite River (SMR) and the Saguenay River sportfishing before December 2001 reported 1402 tagged fish (16.7%). Only three charr were recaptured in estuarine areas out of the Saguenay Fjord. These fish were caught in the St. Lawrence River less than 20 km from the Saguenay River mouth. We did not observe any effect of tagging on growth: length distributions of fish tagged at migration and recaptured 1 year later did not differ significantly from length distribution of untagged fish of the same sea age (May 2000, untagged charr, n = 29, length ± SD = 230.7 ± 42.4, and tagged charr, n = 39, length = 235.6 ± 30.6, t = 0.56, p = 0.58; May 2001, untagged charr, n = 29, length = 220.7 ± 36.3, and tagged charr, n = 49, length = 225.5 ± 22.6, t = –0.73, p = 0.47).

No size-specific mortality following downstream migration was detected. Length distributions at the time of downstream migration of fish tagged during migration and recaptured 1 year later did not differ significantly from length distributions revealed by downstream migration monitoring (Mann–Whitney U test, 1999 downstream migration, 54 recaptures in 2000, p = 0.87, and 2000 downstream migration, 34 recaptures in 2001, p = 0.54). The latter observation also shows the absence of size-specific mortality resulting from tagging.

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Temporal evolution of catches and recaptures of tagged fish according to sea age, maturity stage, and body size

Spring

Temporal patterns of beach seine catches in SMB were similar in 1998, 1999, 2000, and 2001 as far as presence or absence and size of migrants were concerned. Analysis of the evolution of the length of anadromous charr caught in the bay, on a weekly basis, from May to October 1999 and 2000 (the two years in which sampling was the most extensive) revealed that the largest fish were found at the end of April – beginning of May, just after the ice melt (Fig. 5). Sampling of anglers' captures at this time (n = 14, length ± SD = 386.1 ± 64.2 mm; Fig. 6) and analysis of recaptures (Table 1) showed that these charr were mainly sea age 2 migrants and older (representing more than 90% of sampled fish and tag returns in early spring 1999 and 2000). Most of these fish were caught directly at the river mouth and all had the characteristics of kelts that had overwintered in the river after spawning (dark colour, low condition factor, frailty, white flesh, empty and contracted stomachs). All sea age 3 migrants but only 5 of 12 sea age 2 migrants were identified as spawners from the previous year (hook nose in males, well-developed but flabby gonads, presence of a few remaining ovulated eggs in females), and recaptures included fish tagged on the spawning grounds. At the same period, charr of sea age 2 and older were also recaptured in the upstream part of the Saguenay River (essentially in fresh water; Table 1) but were more silvery in colour and in better condition.

From mid-May to the beginning of June 1999 and mid-May to mid-June 2000, we observed a progressive decrease in the length of charr present in the SMB (Fig. 5). This change in length structure corresponded to successive shifts in sea age structure. Firstly, the decrease of maximum observed length in seine hauls (Fig. 5) was associated with a progressive disappearance of the oldest migrants in anglers' captures (Fig. 6) and recaptures (Table 1). Secondly, this period included peak catches of sea age 1 and sea age 2 charr in the SMB (Fig. 6; Table 1). Before the third week of May, sea age 1 migrants were almost exclusively recaptured in the Saguenay River, upstream from the SMB (Table 1). Anglers from the SMB call charr that arrive by mid-May "blue trout" because of their silver-blue colour. They are also characterized by their orange flesh, originating from intensive feeding on marine crustaceans (Geneviève Morinville, Department of Biology, McGill University, Montréal, QC H3A 1B1, Canada, personal communication). Lastly, by the third week of May, migrants-of-the-year entered the bay, which induced a decrease in the mean length of charr caught by seining.

Summer

Significant numbers of migrants-of-the-year were caught by seining in the SMB every week from the third week of May until the last week of July (Fig. 5). On the other hand, some sea age 0 charr left the SMB as soon as the first week of June, migrating to upstream or downstream areas of the Saguenay Fjord, as shown by tag returns (Table 1). Migrants-of-the-year sampled at Anse de Roche (Fig. 1) on 1 and 2 July 1999 were significantly larger than migrants-of-the-year sampled in the SMB on 4 July 1999 (Anse de Roche, n = 83, mean length = 143.2, and SMB, n = 96, mean length = 132.0, Mann–Whitney U test, z = 3.27, p = 0.001). As smaller migrants were not large enough to be targeted by anglers in June and July, we could not use recaptures from the sportfishery to compare the length at tagging of charr that migrated first to deeper, colder, and more saline areas of the Saguenay Fjord with the length of charr that stayed longer in the SMB.

In June and July, we observed a general dispersal of migrants in the Saguenay River (Table 1). However, by mid-July, large charr (FL > 300 mm) started to be caught at Big Pool, in the upstream part of the SMR (Fig. 1). In July and August, all but one charr sampled from anglers' captures in the river had spent at least two growing seasons in the Saguenay River (n = 258, 1998–2001 pooled data). Sea age 2 (and older) migrants were all spawners (n = 153), but only 81% of sea age 1 migrants were sexually mature (n = 104). In August, older migrants (sea age = 2) disappeared from recaptures in the Saguenay River, suggesting that most of them had started their upstream migration to spawning areas by that time of the year. From mid-July until the beginning of September, no tagged fish was caught in the freshwater part of the Saguenay River.

Fall and winter

In September, recaptures of sea age 0 and sea age 1 migrants decreased in areas downstream from the SMB (Table 1). Sea age 1 migrants disappeared totally from recaptures in the Saguenay River and were only observed in the SMB and in the downstream part of the SMR. Captures of sea age 1 charr in these two areas included a few mature individuals (less than 10% every year). These late upstream migrants were significantly smaller than sea age 1 spawners already present in the river during the summer (Table 2). In the same period, sea age 0 juveniles were also observed in the SMB and the SMR. However, tag returns in the upstream part of the Saguenay River indicated that part of the migrants-of-the-year had moved into this freshwater area (Table 1).

The return of some of the juveniles towards the SMR in the fall was associated with an increase of the sportfishery in both the SMB and the SMR. Catches of juveniles were almost completely made up of sea age 0 and sea age 1 migrants (only five catches of immature sea age 2 migrants were recorded in 4 years out of 1546 juveniles sampled in the fall). There were significant differences in length and sea age structures of captures between the SMR and the SMB. Every year and for every sampling period, the length of charr caught in the downstream part of the SMR was significantly greater than the length of charr caught in the SMB (Table 3). The greater body size of charr caught in the river was associated with a higher proportion of recaptures of sea age 1 charr (Table 1), which were larger than migrants-of-the-year in every sampling area (see mean lengths of recaptures in Table 1, $p < 0.01$ in all cases). Sea age 1 charr made up 34% of nontagged juveniles sampled from anglers in the river in 1998 (n = 438), 60% in 1999 (n = 255), and 69% in 2000 (n = 74). In contrast, they constituted only occasional catches in the SMB (Fig. 6). The length of charr caught in the SMB and in the SMR tended to decrease from mid-September until the end of October (Table 3). The parallel

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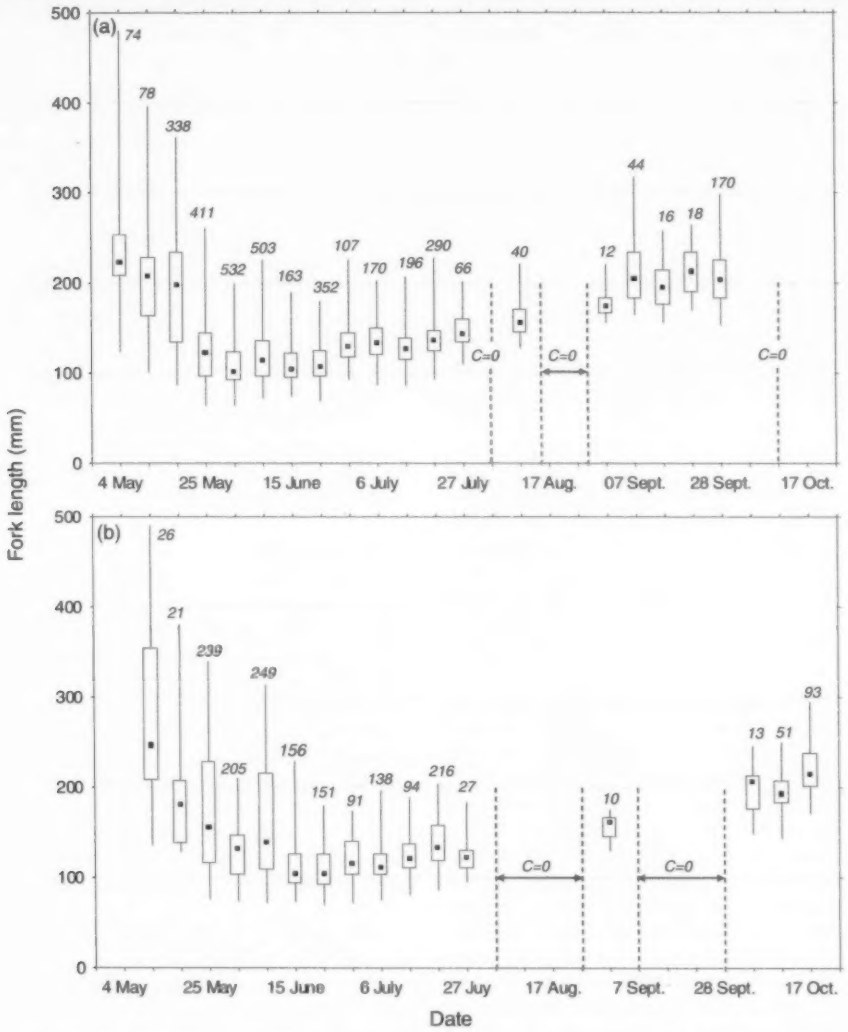
Fig. 5. Temporal evolution of length (median, 25–75% range, total range) of brook charr (*Salvelinus fontinalis*) caught by seining in the Sainte-Marguerite Bay in (*a*) 1999 and (*b*) 2000, on a weekly basis. Numbers in italics are the numbers of charr caught per week (fishing effort was increased when catches were low). "*C* = 0" indicates that no fish could be caught, although fishing effort was maximal.



increase of sea age 0 juveniles in recaptures from the SMR (Table 1) suggests that part of the migrants-of-the-year were leaving the SMB to enter the river. At the end of October, catches of juveniles in the SMB were dominated by small migrants-of-the-year. Stomachs continued to contain prey in almost all charr collected in the SMB in October 1998, 1999, and 2000, whereas at the same periods, less than 52% of the charr collected in the river had stomach contents (Table 4). The end of October was also characterized by a downstream migration of part of the adults after reproduction, as shown by tag returns of postspawners in the downstream part of the SMR and in the SMB (Table 1). Catches of brook charr always decreased in the SMB at the end of October, followed by a usual cessation of the sportfishery.

During winter, we recorded significant tag returns in the freshwater part of the Saguenay River but none in the Saguenay Fjord (Table 1). These recaptures included juveniles (sea age 0 and sea age 1 migrants) and postspawners. Angling was forbidden in the SMR and unusual in the SMB at this time. Sampling in the downstream part of the SMR on 20 February 2000 revealed only the presence of sea age 1 and sea age 2 migrants. Sea age 2 migrants (n = 2) were postspawners but sea age 1 migrants included juveniles (seven out of nine). In 2001, we did not catch any charr in the downstream pools of the SMR. These pools contained large amounts of frazil ice and flow was constrained to narrow high-velocity channels. Two half-day samplings at the river mouth led to the eventual catch of 10 postspawners and four sea age 1 juveniles. The significant number of adults tagged before reproduction in 1999 (n = 463) enabled a comparison between fish that migrated downstream just after reproduction and fish that migrated downstream the following spring. Postspawners recaptured when leaving the SMR in early spring were part of the largest spawners

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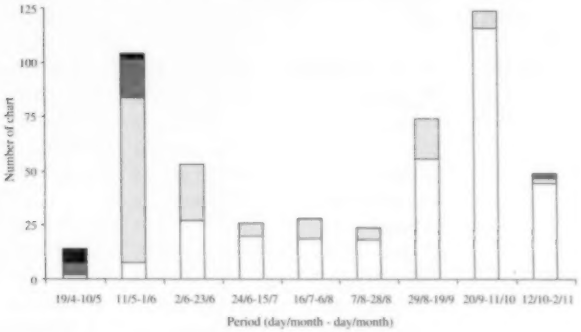
Fig. 6. Number of brook charr (*Salvelinus fontinalis*) subsampled for laboratory analysis while monitoring sportfishery in the Sainte-Marguerite Bay, according to date and sea age (1998–2000, pooled data). Numbers of sampled fish per period were approximately proportional to catches. Percentages of each sea age class for a given period did not differ between years (χ^2, $p > 0.2$ in all cases): 0+, open bars; 1+, lightly shaded bars; 2+, darker shaded bars; 3+, solid bars.



tagged during the previous year and were significantly larger at the time of tagging than postspawners recaptured in the Saguenay River during winter (Fig. 7). Survival from reproduction to the following summer was higher in large than in small spawners tagged in 1999, but we did not observe any size-selective mortality in spawners tagged in 2000 (comparison of the length distributions, at tagging, of all fish tagged and of fish tagged and recaptured the following year: 1999, 463 spawners tagged and 67 recaptures, Mann–Whitney U test, $p < 0.03$, and 2000, 171 spawners tagged and 46 recaptures, Mann–Whitney U test, $p = 0.51$).

As anticipated by the differences in abundance and size of prey in winter between the SMR and the Saguenay River, most of the stomachs collected in the SMR area were empty, whereas 84% of the stomachs collected in the Saguenay River during the same period contained prey (Table 4).

Discussion

The migration patterns of anadromous brook charr from the SMR inferred by the study are presented in Fig. 8. We observed an emigration of migrants-of-the-year in spring during a short period of time. That size of descending charr did not differ between 1999 and 2000 samplings, length distributions were right-skewed in both years, larger charr migrated first, and no size-selective mortality following migration was observed all suggest that there has been selection for a threshold size at first migration. As in other salmonids demonstrating a size-dependent salinity tolerance (and associated survival) (McCormick and Naiman 1984), the growth–mortality trade-off associated with migration to estuarine areas may be negative before charr reach a critical body size. Part of the migrants-of-the-year stayed in the SMB at least until the beginning of August. Others left the bay as soon as early June and dispersed in the Saguenay Fjord. Sea age 0 migrants caught in the fjord in July were significantly larger than sea age 0 migrants caught in the SMB at the same period. Thus, larger migrants left the SMB earlier and (or) growth is enhanced when fish leave the SMB. The study of Montgomery et al. (1990) suggested that larger sea age 0 brook charr moved to deeper and more saline water more readily than did smaller ones. A regular departure of the largest migrants-of-the-year from the SMB would explain why we did not observe any significant increase in the length of fish present in that area in July. Laboratory studies on brook charr have shown that exposure to intermediate salinities before exposure to seawater had a positive effect on survival (McCormick and Naiman 1982) and that salinity tolerance of juveniles increased with body size (Sutterlin et al. 1976; McCormick and Naiman 1984). The prolonged residence of smaller migrants-of-the-year in the SMB (where salinity does not exceed 14‰) may constitute a necessary period of acclimation and growth before entering salt water, as suggested by Montgomery et al. (1990). The major decrease of seine catches in August indicated that most fish had left for the fjord by this time of the summer.

During the fall, migrants-of-the-year moved back towards fresh water. This observation is in accordance with many studies on charr and trout (see Randall et al. 1987) showing a return to the natal river at the end of the summer. However, in our study case, migrants-of-the-year had access to fresh water either in the natal river or in the upstream part of the Saguenay and used both areas. Thus, the tendency of juveniles to return to fresh water in the fall does not appear to involve homing behaviour. As suggested by Dutil and Power (1980), it is more likely that brook charr "sheltered" from the decrease in temperature in the salt water, which can create a severe osmotic stress in this species (Saunders et al. 1975). This hypothesis is particularly relevant in the Saguenay Fjord, where the decrease of temperature in the fall induces a major increase of surface water salinity (up to 22‰). During winter, migrants-of-the-year were still observed in the upstream part of the Saguenay River. As angling stopped in the SMR at the end of October, we only have indirect information about the fate of migrants that moved back to their natal river in the fall. We did not observe any sea age 0 juveniles while sampling in the river or at the river mouth during winter, nor did we observe any significant emigration of sea age 1 charr from the SMR the following spring. Knowing that during the ice-covered period of the Saguenay Fjord, surface temperature stays around 0 °C and surface salinity stabilizes at low values (<7‰), it is possible that after the unfavourable fall period, juveniles descended the river a second time to reach the freshwater part of the Saguenay River. We know that such movements occurred as four juveniles tagged in the SMR in October were caught during the following winter in the upstream part of the Saguenay River. Downstream movements of anadromous brook charr at the end of fall have been observed in other studies (e.g., Smith and Saunders 1958; Castonguay et al. 1982).

Sea age 1 migrants reappeared in the SMB the following spring during a 15-day period starting around May 15. Their good condition and their dark orange flesh suggested that they were already feeding intensively on crustaceans in the fjord when they arrived, in accordance with their probable arrival from upstream areas of the Saguenay River. Sea age 1 migrants left the bay more readily than migrants-of-the-year and occupied all areas of the Saguenay Fjord (including the more saline areas downstream of the SMB) by the beginning

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Table 1. Number and mean length (± standard deviation, mm) of tagged brook charr (*Salvelinus fontinalis*), reported by anglers, according

		Area					
		Saguenay freshwater		Fjord, upstream of SMB		Ste-Marguerite Bay (SMB)	
Date	Sea age	Number	Mean length	Number	Mean length	Number	Mean length
19 Apr. – 10 May	0+	0		0		0	
	1+	4 (0 P-S)	254.3±9.0	4 (0 P-S)	251.0±21.2	1 (0 P-S)	293
	2+	6 (3 P-S)	363.0±47.8	3 (3 P-S)	328.3±36.2	5 (2 P-S)	370.5±20.8
	≥3+	6 (6 P-S)	456.0±72.2	1 (1 P-S)	430	16 (16 P-S)	466.7±49.0
11 May – 1 June	0+	0		0		3 (0 P-S)	154.7±26.9
	1+	4 (0 P-S)	226.4 (1 measured)	2 (0 P-S)	250 (1 measured)	64 (2 P-S)	230.6±29.6
	2+	7 (4 P-S)	355.2±45.7	2 (1 P-S)	355.5±50.2	28 (7 P-S)	341.6±37.8
	≥3+	8 (8 P-S)	446.3±46.0	3 (3 P-S)	469.0±32.6	4 (4 P-S)	435.0±24.3
2 June – 23 June	0+	0		1	153	34	159.4±15.8
	1+	2	266 (1 measured)	8	265.0±42.4	41	231.4±29.7
	≥2+	2	455.5±62.9	2	Not measured	0	
24 June – 15 July	0+	0		5	154.3±27.7	20	159.3±32.0
	1+	1	Not measured	4	270.5±17.8	22	241.7±24.7
	≥2+	2	427.5±50.7	3	382.0±37.0	1	339
16 July – 6 Aug.	0+	0		1 (0 S)	Not measured	25 (0 S)	180.1±26.7
	1+	0		6 (3 S)	298±16.1	21 (1 S)	249.7±23.7
	≥2+	0		0		2 (2 S)	320.5±30.4
7 Aug. – 28 Aug.	0+	0		4 (0 S)	197.5±22.8	29 (0 S)	189.8±24.7
	1+	0		0		7 (0 S)	266.5±17.2
	≥2+	0		0		0	
29 Aug. – 19 Sept.	0+	2 (0 S)	234 (1 measured)	4 (0 S)	238.3±23.2	73 (2 S)	213.5±32.5
	1+	0		0		14 (1 S)	285.4±23.4
	≥2+	0		0		1 (0 S)	340
20 Sept. – 11 Oct.	0+	9 (0 S)	229.7±30.6	3 (0 S)	191.0±3.6	96 (0 S)	229.9±26.7
	1+	0		0		21 (0 S)	294.8±31.7
	≥2+	0		0		0	
12 Oct. – 1 Nov.	0+	18 (0 P-S)	224.2±35.1	0		33 (0 P-S)	224.4±24.1
	1+	0		0		8 (4 P-S)	283.4±33.4
	≥2+	0		0		2 (2 P-S)	472.5±60.1
2 Nov. – 18 Apr.	0+	44 (0 P-S)	246.4±30.6	1 (0 P-S)	Not measured		
	1+	30 (17 P-S)	354.8±27.6	0		No angling	
	≥2+	10 (10 P-S)	428.8±50.3	0			

Note: Data were pooled over the 1999–2001 experimental period. Tag return rates at a given sea age were similar every year. Fish recaptured less than sea age classes, but comparisons may be made between cells, except those including sea age 0 charr in May–July, because their size is too small for the

of June. Some of the sea age 1 charr were mature and migrated to spawning areas from mid-July to September, larger ones returning to the river earlier in the summer. However, even immature sea age 1 migrants moved back to the river at the end of the summer. They dominated captures of juveniles in the SMR in the fall of 1999 and 2000 and were never observed in the upstream part of the Saguenay River during that period, unlike migrants-of-the-year. We also had evidence that part of them actually overwintered in the SMR and waited until the following spring to move back to the Saguenay Fjord. These observations are in accordance with the study of Castonguay et al. (1982), which suggested that migration patterns of sea age 0 and sea age 1 juvenile brook charr are different in some populations.

The analysis of stomach contents confirmed that food was still abundant in the Saguenay River in winter and that fish present in the Saguenay during that period fed more than fish present in the SMR. Whether or not smaller migrants may face starvation if staying in the SMR in winter is not known. Starvation risk may oblige migrants-of-the year to overwinter in the Saguenay, where the increased costs associated with variable abiotic conditions and higher predation risk would be compensated by greater growth opportunities. The fact that sea age 0 charr overwinter in the Saguenay may also reflect a more risky behaviour of these fish to maximize growth during their first year in salt water to increase the probability of reproducing the next fall. It could be the case of an environment selecting for early maturation (for instance, where adult survival is low relative to juvenile survival (see Stearns 1992)). In contrast, sea age 1 juveniles adopted a more conservative behaviour: they returned to the SMR earlier in the fall and a significant portion of them stayed there untii the following spring. This observation is in accordance with our prediction, coming from Clark's (1994) asset-protection principle: at the end of their second growing season in estuarine areas, charr give priority to increasing survival by sheltering instead of increasing growth in a riskier environment. In the fall, sea age 1 charr are larger than migrants-of-the-year. Size is intimately connected with reproductive success in salmonids as fecundity of fish gener-

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to date, sea age, and fishing area.

Fjord, downstream of SMB		Ste-Marguerite River downstream		Ste-Marguerite River upstream	
Number	Mean length	Number	Mean length	Number	Mean length
0					
1 (0 P-S)	240				
0		No angling		No angling	
0					
0					
10 (0 P-S)	216.5±27.2				
3 (0 P-S)	359.7±48.6	No angling		No angling	
2 (2 P-S)	481.5±0.7				
6	166.7±14.6	0		0	
27	246.5±23.7	0		0	
18	422.9±48.3	0		0	
12	172.7±28.7	0		0	
31	273.6±32.4	0		0	
7	408.8±48.3	0		1 (1 S)	466.6
12 (0 S)	188.2±15.2	0		0	
20 (3 S)	283.4±19.8	0		9 (8 S)	353.1±22.7
2 (2 S)	338 (1 measured)	0		9 (9 S)	445.0±61.4
17 (2 S)	205.8±28.7	0		1 (1 S)	209
6 (4 S)	304.8±22.0	0		11 (7 S)	349.0±16.1
0		0		23 (23 S)	434.5±60.8
12 (0 S)	208.0±23.1	1 (0 S)	220	0	
4 (0 S)	261.7±12.6	21 (4 S)	302.1±33.9	13 (12 S)	330.4±46.1
0		0		25 (25 S)	426.2±45.3
0		38 (0 S)	240.6±18.9		
0		63 (4 S)	306.5±31.5	No angling	
0		0			
0		48 (0 P-S)	251.5±26.2		
0		35 (10 P-S)	321.3±34.3	No angling	
0		22 (22 P-S)	434.4±45.9		
0					
0		No angling		No angling	
0					

2 weeks after tagging were omitted. Proportions of recaptures according to sea age do not represent absolute proportions of sportfishery. SMB, Ste-Marguerite Bay; S, spawners; P-S, postspawners.

Table 2. Length (mean ± standard deviation, mm) of sea age 1 brook charr (*Salvelinus fontinalis*) spawners sampled while monitoring sportfishery in the upstream part of the Sainte-Marguerite River (SMR upstream) during the summer and in the Sainte-Marguerite Bay (SMB) and the downstream part of the Sainte-Marguerite River (SMR downstream) in the fall in 1998, 1999, and 2000.

Year	SMR upstream, summer	SMB and SMR downstream, fall	Student's *t* test results
1998	326.9±31.0 (n = 14)	303.1±18.6 (n = 12)	$p < 0.03$
1999	343.6±26.3 (n = 17)	314.5±28.0 (n = 15)	$p < 0.05$
2000	345.5±28.1 (n = 19)	284.9±28.6 (n = 13)	$p < 0.0001$

ally increases with body size and because a larger size may constitute an advantage in territorial competitions at the time of reproduction (Dodson 1997). Thus, without considering age at maturity, sea age 1 migrants have greater reproductive assets to protect than migrants-of-the-year. In addition, sea age 1 charr (having reached size at maturity) will reproduce the following fall, which is not the case of many migrants-of-the-year. Therefore, in terms of time to elapse before reproduction, sea age 1 charr have greater reproductive prospects to protect than migrants-of-the-year. The more conservative behaviour of older juveniles may be limited by energy constraints, as suggested by the arrival of some sea age 1 juveniles in the Saguenay River during winter. A portion of sea age 1 juveniles may not have had sufficient energy reserves to spend winter without feeding and (or) to reproduce the following year.

Charr having spent more than two growing seasons in the Saguenay River showed migration patterns very similar to

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Table 3. Length (mean ± standard deviation, mm) of juvenile brook charr (*Salvelinus fontinalis*) measured while monitoring sportfishery in the fall in 1998, 1999, and 2000, according to area and period.

		Area	
Year	Period	Ste-Marguerite Bay	Ste-Marguerite River
1998	29 Aug. – 19 Sept.	241.7±48.8a (n = 36)	286.3±36.9b (n = 188)
	20 Sept. – 11 Oct.	235.3±28.7a (n = 109)	270.4±39.8c (n = 415)
	12 Oct. – 2 Nov.	228.6±20.3a (n = 19)	265.6±33.6d (n = 515)
1999	29 Aug. – 19 Sept.	238.3±32.7a (n = 39)	295.4±41.8c1(n = 139)
	20 Sept. – 11 Oct.	238.6±34.9a (n = 220)	299.9±43.8c2 (n = 441)
	12 Oct. – 2 Nov.	226.3±22.9b (n = 59)	292.8±52.7c1, d2 (n = 285)
2000	29 Aug. – 19 Sept.	259.1±36.8a (n = 28)	301.2±37.4c (n = 39)
	20 Sept. – 11 Oct.	272.0±39.8a (n = 42)	297.7±46.1c (n = 324)
	12 Oct. – 2 Nov.	220.5±27.6b (n = 18)	290.6±53.3c (n = 55)

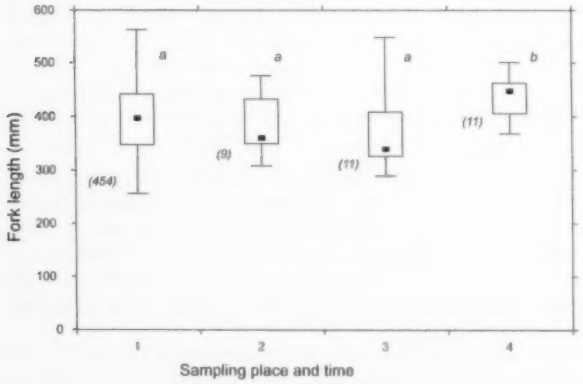
Note: For a given year, different letters (associated with a given number if need be) indicate significant difference at p = 0.05 (Student's t test).

Table 4. Percentage of stomachs with contents in brook charr (*Salvelinus fontinalis*) sampled in the fall and winter, according to area.

Season	Sampling site	Period	N	Percentage of stomachs with contents
Fall		Oct. 1998	48	93.8
	SMB	Oct. 1999	42	92.9
		Oct. 2000	14	100
		Oct. 1998	238	43.3
	SMR	Oct. 1999	168	48.8
		Oct. 2000	47	51.1
Winter	Saguenay	Jan.–Feb. 2000	11	62.5
	Saguenay	Jan.–Feb. 2001	11	100
	SMR	Feb. 2000	11	0.9
	SMR (mouth)	Feb. 2001	12	33.3

Note: SMB, Sainte-Marguerite Bay; SMR, Sainte-Marguerite River (Geneviève Morinville and Joe Rasmussen, Department of Biology, McGill University, Montreal, QC H3A 1B1, Canada, unpublished data).

Fig. 7. Length at tagging (median, 25%–75% range, total range) of (1) all brook charr (*Salvelinus fontinalis*) spawners tagged at the Big Pool during summer 1999 and (2–4) spawners tagged at the Big Pool in 1999 and recaptured migrating downstream the Sainte-Marguerite River in October (2), recaptured while overwintering in the Saguenay River (3), and recaptured in the Sainte-Marguerite Bay in spring 2000 (4). Samples sizes are given in brackets. Different letters indicate significant difference at p = 0.05 (Mann–Whitney U test).



sea age 1 charr, except that they were almost all mature and undertook their upstream migration to spawning areas early in the summer. After reproduction, some left the SMR to overwinter in the upstream part of the Saguenay River, whereas some overwintered in the SMR. The mark–recapture experiment carried out on adults present on spawning grounds (including some of sea age 1 migrants) showed that postspawners leaving the SMR in early spring were part of the largest spawners tagged during the previous year and were significantly larger, at the time of tagging, than postspawners recaptured in the Saguenay River during winter. This observation was associated with a higher mortality in smaller adults. Therefore, the larger size of fish leaving the SMR in early spring may be the result of two phenomena that are not mutually exclusive: smaller postspawners exhibit a greater probability of mortality if they remain within the SMR and smaller postspawners exhibit a greater probability of outmigration from the SMR to exploit the richer feeding areas of the Saguenay River in winter. Both scenarios suggest that smaller adults face higher energy constraints following reproduction. As such, larger adults may be behaving conservatively by remaining sheltered in the river during the winter following reproduction, whereas smaller adults are obliged to feed in the Saguenay immediately after reproduction.

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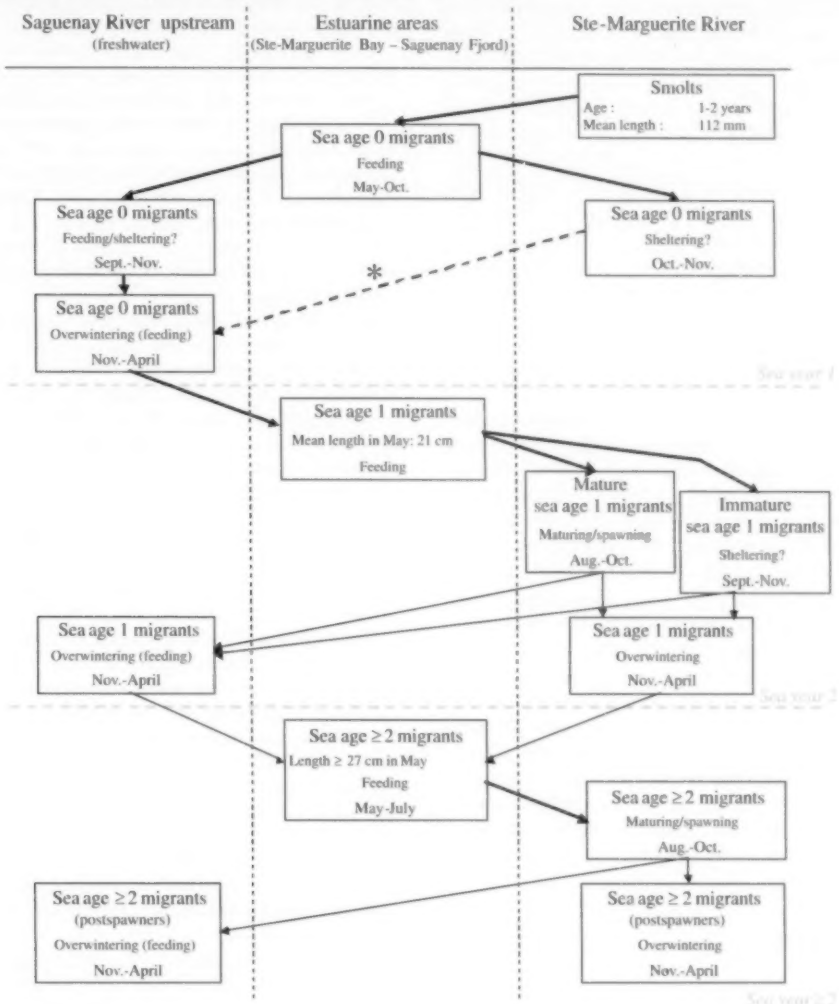
Fig. 8. Schematic model for the migratory patterns of anadromous brook charr (*Salvelinus fontinalis*) from the Sainte-Marguerite River, Saguenay, Québec, Canada, according to sea age and maturity stage. *, inferred.



Finally, we had evidence that abiotic factors may affect the seasonal behaviours of anadromous brook charr. The presence of large amounts of frazil ice during winter 2001 seemed to have driven fish towards the river mouth. A telemetry study on winter movements of cutthroat trout showed that fish moved downstream when their habitat was affected by frazil and anchor ice (Brown 1999). In Ellerslie Brook (Prince Edward Island), major outward movements of brook charr at 0 °C may be associated with the formation of frazil ice (Smith and Saunders 1958). Frazil ice represents a major danger for fish (which may be affected by ice crystals in their mouth and gills), limits available habitat, and constrains flow to channels where velocity may be too high for fish to maintain position (see references in Brown 1999). The fact that 2000 spawners overwintering in the river had to leave it may explain why we did not observe any size-specific mortality in tagged fish, as mortality risk was high for both small and large postspawners.

Growth rate and mortality risk in fresh water and estuarine areas will change according to specific environmental settings. Migratory behaviour of brook charr populations should reflect local opportunities and constraints. For instance, age at first downstream migration tends to increase with latitude (Castonguay et al. 1982). This latitudinal cline could result from slower growth in northern rivers (e.g., Dutil and Power 1980), where charr need a longer stay in fresh water to reach the size at first migration observed in southern rivers (e.g., White 1940). However, brook charr from the SMR migrate earlier and at smaller size than brook charr from the Moser River, Nova Scotia (ages 2 and 3, modal sizes 170–200 mm; White 1940), located south of the SMR, or than brook charr from the Saint-Jean River, Québec (ages 2 to 4, 100–200 mm; Castonguay et al. 1982), located at a similar latitude. If the existence of a threshold size at first migration is associated with the size-dependent salinity tolerance of brook charr, a smaller size at downstream mi-

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gration in the SMR may be explained by the low salinity of the SMB (<5.5‰ in spring). Comparable sizes of smolts, associated with low salinity conditions, were also observed in the Moisie River estuary (Montgomery et al. 1990). Similarly, the thermohaline stratification of the Saguenay River may promote the long distance movements (as far as 100 km) of juveniles and adults rarely observed in other populations (see Power 1980). This could be especially true in winter; in populations of brook charr observed overwintering outside their natal river, those fish caught were only a short distance from the river mouth (e.g., Smith and Saunders 1958; Castonguay et al. 1982). A low age at downstream migration and an intense exploitation of estuarine areas in brook charr from the SMR is associated with fast growth and a low age at maturity (3+) relative to other populations from Québec and the Maritimes (see Power 1980; Castonguay et al. 1982), emphasizing the link between migratory behaviour and other life-history traits.

In summary, our results showed that if anadromous behaviour depends on a growth–mortality trade-off, it is dynamic in nature. Migratory patterns of brook charr from the Sainte-Marguerite River imply that fitness payoffs in river and estuary may vary according to time of year, growth, maturity stage, and condition of individuals. As predicted by behavioural models, migratory patterns of charr changed throughout their ontogeny, and as fish grew and accumulated fitness assets, they tended to adopt a more conservative behaviour. Factors affecting migration may have an effect on other life-history traits and vice versa. Environmental differences related to geographical location can be responsible for the variation of migration patterns and life histories that we commonly observe within salmonid species or between closely related ones. Accurate knowledge of the influence of environmental factors on growth and mortality of salmonids is necessary to fully understand the link between migratory behaviour and the life history of anadromous species.

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An analysis of homogenization and differentiation of Canadian freshwater fish faunas with an emphasis on British Columbia

Eric B. Taylor

Abstract: Faunal homogenization and differentiation occur when geographic regions show increased or decreased, respectively, similarity to each other in species composition owing to introductions and extinctions or extirpations. I used species presence–absence data for "native" (i.e., estimated species compositions before European settlement) and "total" (i.e., including nonnative fishes and extinctions) faunas to examine faunal similarity of freshwater fishes among aquatic ecoregions of British Columbia and among Canadian provinces and territories. British Columbia ecoregions showed faunal differentiation as the mean Jaccard's faunal similarity coefficient for total faunas was significantly less than that for native faunas (31.4% versus 34.9%), but some ecoregions showed homogenization (e.g., Vancouver Island and Columbia River ecoregions). Comparisons across Canada showed low but significant homogenization; average pairwise Jaccard's coefficient was higher in total versus native faunas (29.1% similarity versus 27.8%, respectively). British Columbia's fish fauna increased the most in similarity to other areas (except the three territories), with an average increase of 4.9%. Native faunal similarity patterns are part of Canada's natural heritage but are threatened by human-mediated increases in nonnative species and extinctions. This analysis provides a baseline to track changes in inter-regional faunal relationships at different geographic scales.

Résumé : L'homogénéisation et la différentiation de la faune se produisent lorsque des régions géographiques présentent des compositions spécifiques respectivement plus semblables ou moins similaires à cause d'introductions ou d'extinctions ou extirpations. Des données de présence–absence sur les faunes « indigènes » (i.e., les compositions spécifiques estimées d'avant l'arrivée des européens) et « totales » (i.e., incluant les espèces introduites et les espèces disparues) m'ont permis de comparer la ressemblance des faunes de poissons d'eau douce dans les écorégions aquatiques de Colombie-Britannique et dans les provinces et territoires canadiens. Il y a de la différentiation faunique parmi les écorégions de la Colombie-Britannique puisque le coefficient de similarité de Jaccard moyen de la faune totale est significativement moins élevé que celui de la faune indigène (31,4 % par rapport à 34,9 %), mais quelques écorégions présentent une homogénéisation (e.g., les écorégions de l'île de Vancouver et du fleuve Columbia). Les comparaisons à l'échelle du Canada indiquent une homogénéisation faible, mais significative, et les coefficients de Jaccard moyens appliqués deux à deux sont plus élevés pour la faune totale que pour la faune indigène (une similarité de 29,1 % par rapport à 27,8 %). Par comparaison aux autres régions, mais à l'exception des trois territoires, c'est en Colombie-Britannique que la similarité de la faune de poissons a augmenté le plus, en moyenne de 4,9 %. Les patterns de similarité faunique indigène font partie de l'héritage naturel du Canada, mais ils sont menacés par des augmentations du nombre d'espèces non indigènes et des extinctions causées par les humains. Cette analyse fournit une base pour l'observation des changements dans les relations fauniques inter-régionales à différentes échelles géographiques.

[Traduit par la Rédaction]

Introduction

Freshwaters contain some of the most threatened faunas in the world and are estimated to have the highest recent and projected future extinction rates in North America (Riccardi and Rasumssen 1999). These faunas have generally suffered from elevated extinction rates owing to anthropogenic factors such as overexploitation, habitat degradation, so-called "chains of extinction", and the introduction of exotic species (Rhymer and Simberloff 1996). The introduction of nonnative species may result in extinctions of native species via predation, disease transmission, competition, habitat modification, or hybridization. In addition, even if nonnative species do not cause the extinction of native species, they can change the natural patterns of species diversity within geographic areas as well as the zoogeographic relationships among areas. One such change to faunal composition from the single or combined effects of introductions and extinctions or extirpations is known as "homogenization", where regional faunas become more similar to each other over time

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(Rahel 2002). A recent study of freshwater fish faunas in the United States (excluding Alaska and Hawaii) found that widespread introductions had resulted in an average increase in Jaccard's faunal similarity of 7.2% (Rahel 2000). Other studies in individual states have found similar results for fish and other aquatic taxa and also that the degree of homogenization may be dependent on the geographic scale examined (e.g., Marchetti et al. 2001; reviewed in Rahel 2002). By contrast, faunal "differentiation" may be defined as the case in which faunas become less similar to each other from the same causes, but this phenomenon has received little examination.

Homogenization is an important phenomenon to document and track because it represents a clear case of the loss of worldwide biodiversity in several ways (Wilson 1988; Marchetti et al. 2001). First, homogenization may involve extinction of species endemic to particular regions (Rahel 2002). Second, homogenization represents a loss of beta species diversity, or the turnover of species between geographic areas. The loss of beta diversity results because more species become common to different areas resulting in reduced turnover between geographic areas. Third, homogenization results in a loss of the zoogeographic "individuality" of geographic regions, as measured by native faunal uniqueness, and may change faunal relationships among areas. The natural faunal composition of a particular region results from an interplay between historical contingencies and the past and current ecological, physiological, and life history attributes of particular taxa and their interactions with other taxa. Such interactions are part of the faunal legacy of particular areas and, therefore, have inherent conservation value. The loss of diversity through homogenization also represents lost opportunities for use by humanity, as well as the potential for disruption of ecosystem services (Rahel 2002). Notwithstanding arguments concerning the potential benefits of human-induced changes in biodiversity, informed assessments of such debates cannot take place without first documenting faunal composition changes and their effects on aesthetic values and natural processes such as ecosystem stability and services.

The phenomenon of homogenization has received considerable attention in the United States (U.S.), but there have been no formal treatments of similar phenomena in Canada, despite an appreciation of the generally negative impacts of introductions and extinctions (e.g., Crossman 1991). Canada, however, is the second largest country in the world and contains over 890 000 km^2 of freshwater habitat. In particular, British Columbia (B.C.) is Canada's third largest province and has an abundance of freshwater habitats that include or form part of some of the largest drainage basins in North America (e.g., the Fraser, Mackenzie, Columbia, and Yukon river systems). These watersheds drain a vast area from the Arctic Ocean to the mid-temperate Pacific Ocean, and their sundering by extensive mountainous terrain promotes a high level of faunal distinctiveness among regions (McPhail and Carveth 1994). In addition, the freshwater fish fauna of B.C. is almost exclusively postglacial in origin, freshwater faunas having recolonized B.C. from glacial refugia located peripheral to the Wisconsinan ice sheets after they retreated beginning about 18 000 years ago (Lindsey and McPhail 1986; McPhail and Lindsey 1986). The recent origin of the B.C. freshwater fauna means that many ecosystems may not yet be at equilibrium species diversity and could be particularly sensitive to the effects of homogenization from increases in nonnative species and extinctions.

In this study, I provide a summary of fish introductions and extinctions or extirpations in B.C. by major aquatic ecoregion and conduct faunal similarity analyses to test for homogenization within B.C. I then provide a similar analysis at a larger geographic scale that includes the nine other provinces and three territories to test for homogenization for the Canadian fauna as a whole.

Materials and methods

The primary data for my analyses consisted of presence–absence information for the 82 taxonomically recognized fish species in B.C. and the 218 recognized species in Canada (i.e., native and nonnative species; presence–absence matrices are available from the Depository Unpublished Data of the National Research Council of Canada[1]). By "taxonomically recognized", I refer only to those species that have been given formal Linnaean classification. For instance, in B.C., I used "*Gasterosteus aculeatus*" (threespine stickleback) as a single species even though it is part of a complex that probably consists of several undescribed species, e.g., the benthic–limnetic species pairs (McPhail 1994). Although utilizing only formally described taxa in my analyses is an imperfect measure of fish biodiversity, there is no formal consensus on species status for such cases in sticklebacks or, indeed, for other taxa in which similar species complexes occur (e.g., sockeye salmon and kokanee (*Oncorhynchus nerka*) and normal and dwarf lake whitefish (*Coregonus clupeaformis*)), and the greatest depth of divergence in freshwater fishes is probably adequately represented by the formally described taxa. In addition, I included diadromous fishes, such as Pacific (*Oncorhynchus* spp.) and Atlantic (*Salmo salar*) salmon and American eels (*Anguilla rostrata*), which complete portions of their life history and may reside for extended periods in freshwater. I did not, however, include marine fishes that may occasionally be found in rivers that drain to the sea (e.g., fourhorn sculpin (*Myoxocephalus quadricornis*) in Ontario, Manitoba, and Quebec and Pacific staghorn sculpin (*Leptocottus armatus*) in B.C.).

The presence–absence data in B.C. were listed by the eight major aquatic ecoregions (Fig. 1) based on the classification of McPhail and Carveth (1994). These ecoregions represent the major drainage basins, or sets of smaller drainages, in B.C. defined by current or historical connectedness, isolation by saltwater barriers, and colonization from similar glacial refugia (McPhail and Carveth 1994): Vancouver Island and adjacent Strait of Georgia islands, Fraser River, Columbia River, Mackenzie River, Yukon River, North Coast (Stikine, Alsek, and Taku rivers), Queen Char-

[1] Supplementary data for this article are available on the Web site or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2, Canada. DUD 3540. For more information on obtaining material refer to http://www.nrc-cnrc.gc.ca/cisti/irm/unpub_e.shtml.

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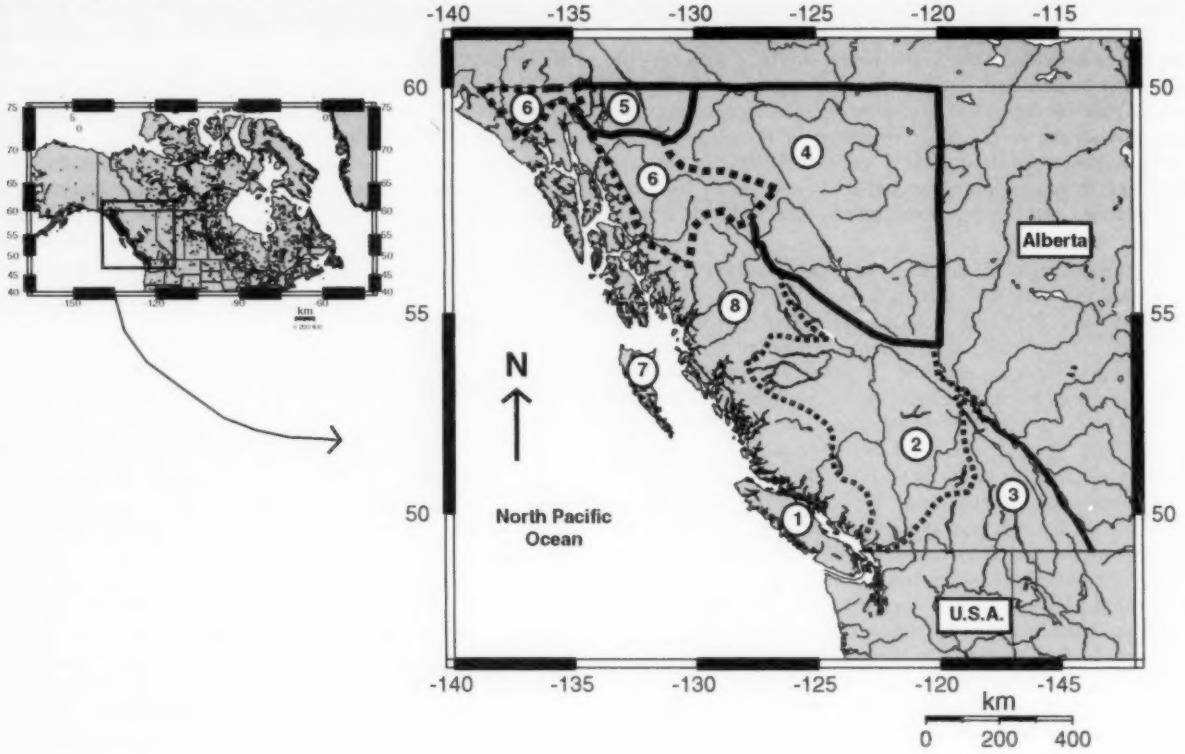
Fig. 1. Aquatic ecoregions of British Columbia, Canada: 1, Vancouver Island; 2, Fraser River; 3, Columbia River; 4, Mackenzie River; 5, Yukon River; 6, North Coast; 7, Queen Charlotte Islands; 8, Central Coast. (Modified from McPhail and Carveth (1994).)



lotte Islands, and the Central Coast (Skeena and Nass rivers). Some of these regions are part of larger drainage systems that extend beyond the borders of B.C. (i.e., the Yukon, Columbia, and Mackenzie river ecosystems), but the current analysis refers only to those portions within B.C. Presence–absence data were obtained from McPhail and Carveth (1994) and, in some cases, records from the University of British Columbia Fish Museum (see http://www.zoology.ubc.ca/~etaylor/nfrg/fishmuseum.html) and the B.C. Ministry of Water, Land and Air Protection (BCWLAP; E. Parkinson, Biodiversity Branch, B.C. Ministry of Water Land and Air Protection, 2204 Main Mall, University of British Columbia, Vancouver, BC V6T 1Z4, personal communication). Presence–absence data for the nine other provinces and three territories were based on information from the Wild Species 2000 database available at http://www.wildspecies.ca (Canadian Endangered Species Conservation Council (CESCC) 2001). The wild species database was generated by a national working group composed of representatives from all provinces and territories and two federal government agencies, Environment Canada (Canadian Wildlife Service) and Fisheries and Oceans Canada. These data were subjected to extensive review by the working group and are considered to be the result of the "best available" published and unpublished information as of 2000 (Kent Prior, Species at Risk Branch, Canadian Wildlife Service, Environment Canada, 351 St. Joseph Boulevard, Hull, QC K1A 0H3, personal communication). Other major sources of information included national and regional summaries such as Nelson and Paetz (1992) and Scott and Crossman (1998). A complete listing of authorities consulted is available from the author.

Various definitions have been proposed to differentiate kinds of nonnative fishes, usually on the basis of geographic origin or the process of establishment (e.g., Shafland and Lewis 1984; Crossman 1991). In my analyses, a "native" species is defined as one that occurs, or occurred historically, in a defined area as a result of natural processes exclusive of any influence from humans. A "nonnative" species is defined as one that occurs in an area via the direct (e.g., via deliberate introductions) or indirect influence of humans (e.g., natural dispersal into one area as a result of introduction into an adjacent area). For instance, I included all sources of nonnative species whether they were intentionally or accidentally introduced into an area or whether their occurrence in one area is the result of dispersal from nonnative populations in an adjacent area (e.g., *Stizostedion vitreum* in the lower Columbia River basin in Canada). Because my primary interest was in testing for changes to native fish assemblages, I adopted the term "nonnative", rather than more restrictive terms such as "exotic", "invasive", or "transplanted" (see also Horak 1995) to encompass in a single term the variety of processes that may have led to nonnative species. "Introductions" or "introduced" refers to the action of becoming a nonnative fish via the direct or indirect effects of humans. A nonnative species was included in the analyses

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if there was at least some evidence that it had established a breeding population(s) and (or) has been repeatedly encountered in nature in the ecoregion, province, or territory (e.g., from persistent introductions). Finally, despite extensive review of the database, there will always be some uncertainty about the true absence or presence of some species in particular areas, particularly at the national level. This is largely a function of differences in opinion, even among experts (personal observation), and the inherent difficulty of proving absence of a taxon after it has been reported. The analyses that follow, however, were completed with and without these taxa ($N = 7$), and their elimination from the database did not change the general results or statistical significance of my analyses.

The presence–absence (1,0) data were summarized by calculating pairwise Jaccard's coefficient of percentage faunal similarity:

$$J = [a/(a + b + c)] \times 100\%$$

where a is the number of species shared between any two regions being compared, b is the number of species found only in the first area, and c is the number of species found only in the second area (Jaccard 1908; Rahel 2000). I also calculated an index of faunal turnover between areas within B.C. and between all provinces and territories by calculating one estimate of beta diversity (percentage faunal turnover between any two regions):

$$T = [(a + b)/c] \times 100\%$$

where a is the number of species unique to the first area, b is the number of species unique to the second area, and c is the total species pool (Rahel 2002). In the classic sense, faunal turnover refers to the change in species composition along a transect that passes through adjacent areas. In the present context, however, I employed it simply as a measure of faunal distinctiveness between areas that are not necessarily contiguous. Calculation of these statistics was accomplished, in part, using EstimateS software written by R.K. Colwell and available at http://viceroy.eeb.uconn.edu/estimates.

Pairwise similarity and turnover indices were calculated separately for native faunas, faunas before known introductions or extinctions or extirpations associated with European settlement (cf. Rahel 2000; Marchetti et al. 2001), and for total faunas, native and nonnative species minus any extinctions or extirpations. Faunal similarity among regions was summarized by clustering estimates of Jaccard's similarity coefficient (subtracted from 1.0 to generate a "distance" measure) and turnover coefficients using the neighbor-joining (NJ) algorithm (Saitou and Nei 1987). Presence–absence data, however, are an incomplete estimate of fish faunal diversity because they do not take into account the abundance of species in particular areas. In some cases, for instance, species are recorded as present in a particular area based on one or a few records only. To obtain some estimate of the robustness of ecoregion relationships based on faunal similarity, the presence–absence matrix was subjected to parsimony analysis of endemism (PAE). Rosen (1984) first applied PAE to species presence–absence data to assess area relationships based on shared presence of taxa, and it has been subsequently applied to a number of different taxa including freshwater fishes in other areas (Da Silva 1996; Watanabe 1998; Unmack 2001). Preliminary analyses indicated that applying Wagner parsimony analysis, in which species extinctions or extirpations or colonizations are equally probable, to the presence–absence matrix resolved the same topologies as NJ clustering of Jaccard's coefficient. Consequently, the presence–absence matrix was subjected to bootstrap resampling ($N = 100$) to simulate the effects of variation in species sampling on the resulting faunal similarity matrices used in the clustering analyses. These bootstrapped matrices were then used in Wagner parsimony analyses, and a consensus tree was derived using the Mix and Consense programs of Phylip (Felsenstein 1995).

Species numbers, pairwise Jaccard's and turnover coefficients, and changes in faunal similarity for B.C. were correlated with independent variables using simple parametric or rank correlations and Mantel tests (Manly 1997), as implemented in Systat (Systat Software Inc., Richmond, Calif.) and Genepop (version 3.3; Raymond and Rousset 2001). Possible explanatory variables investigated included ecoregion drainage area and geographic distance between the geographic centre of each ecoregion. These variables were estimated from topographic maps. Differences between native and total faunal pairwise Jaccard's and turnover coefficient matrices were tested by Fisher's paired comparison randomization test with 10 000 randomizations as implemented by the Rundum software package (version 1.0; Jadwiszczak 2002). In these tests, pairwise observations of Jaccard's or turnover coefficient are randomly assigned to native and total faunal groups and the difference between each pairwise comparison is computed. The mean of these randomized paired comparisons is assessed against the observed mean difference and the latter is declared significant if it is more extreme than 95% or more of the values in the randomized distribution.

Results

British Columbia freshwater fishes

The native freshwater fish fauna of B.C. consists of 66 species and varies from a low of 14 species in the Queen Charlotte Islands to a high of 42 species in the Fraser River ecoregion (Table 1). The total number of historical native species was positively correlated with drainage area ($r = 0.94$, $P = 0.001$). There is only a single recorded extinction–extirpation within any of these eight drainage areas: chinook salmon (*Oncorhynchus tshawytscha*) that once returned to spawn in tributaries of Columbia Lake in the headwaters of the Columbia River were extirpated from the Canadian portion of the Columbia drainage by the construction of the Grand Coulee Dam in Washington State in 1941. By contrast, B.C. now contains a total of 21 species that are nonnative to at least one ecoregion: 15 species originated from outside the province and six species originated from one or more other B.C. ecoregions. The Columbia River drainage has the most nonnative fishes (16) and the Queen Charlotte Islands and the Yukon River are the only B.C. aquatic ecoregions without nonnative species (Table 1). After including nonnative fishes and extinctions or extirpations, total species number was also positively correlated with drainage area ($r = 0.95$, $P < 0.001$).

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Table 1. Names, approximate drainage areas, and numbers of native, nonnative, extirpated, and total freshwater fish species in the eight aquatic ecoregions of British Columbia.

Aquatic ecoregion	Drainage area (km^2)	No. of historical native species	No. of extant nonnative species	No. of extirpated species	Total no. of extant species
Queen Charlotte Islands	14 500	14	0	0	14
Yukon River	25 000	16	0	0	16
Vancouver Island	32 000	16	8	0	24
North Coast	83 800	29	1	0	30
Columbia River	116 300	27	16	1	42
Central Coast	204 900	31	1	0	32
Fraser River	233 000	42	10	0	52
Mackenzie River	285 900	39	4	0	43

Note: The total number of extant species is equal to the total number of historical native species minus any extinctions or extirpations, plus nonnative species. Species distributions and ecoregion definitions are from McPhail and Carveth (1994).

Jaccard's similarity indices of native faunas ranged from a low of 6.6% between the Yukon drainage and the Queen Charlotte Islands to a high of 76.5% between Vancouver Island and the Queen Charlotte Islands (Table 2; Fig. 2*a*). Neighbor-joining clustering of distances based on these indices revealed three major ecoregion groupings: Vancouver Island – Queen Charlotte Islands, North–Central coasts and the Fraser River, and a heterogeneous mixture of the Yukon, Mackenzie, and Columbia rivers (Fig. 3*a*). Estimates of faunal turnover ranged from a low of 13.3% between Vancouver Island and the Queen Charlotte Islands to a high of 86.5% to 87.5% between these two island ecoregions and the Yukon ecoregion. Faunal turnover coefficients resolved the same ecoregion affinities as Jaccard's coefficient (not shown). B.C. native freshwater fish faunas became less similar to one another as the distance between their geographic centres increased ($r = -0.31$, Mantel test, $P = 0.02$), and faunal turnover increased with geographic distance ($r = 0.47$, $P = 0.02$).

After incorporating nonnative species and extinctions or extirpations, pairwise Jaccard's coefficient ranged from a low of 5.3% between Vancouver Island and the Yukon ecoregions to a high of 72.2% between the North Coast and Central Coast ecoregions (Table 2; Fig. 2*b*). Clustering these estimates resulted in ecoregion affinities similar to those resolved by comparing native faunas but revealed evidence of increased differentiation of ecoregions (Fig. 3*b*). For instance, the average pairwise change in Jaccard's coefficient was a decrease of 3.5% (34.9% to 31.4%) and the pairwise native and total Jaccard's coefficient matrices were significantly different from one another (matrix randomization test, $P = 0.017$; Figs. 2, 4). The greatest percentage decline in similarity occurred between Vancouver Island (eight nonnative species) and the Queen Charlotte Islands (no nonnative species), where Jaccard's index fell from 76.5% to 51.9% similarity (–23% of native value). The same large number of nonnative species on Vancouver Island, coupled with those in the Columbia basin (16 nonnative species), resulted in the largest percentage increase in similarity between any two regions, i.e., from 13.2% to 20.1% (52% of native faunal value). The only other pairwise comparison to show substantial faunal homogenization was that between the Columbia River and the Mackenzie River drainage, where Jaccard's coefficient showed a 21.1% increase relative to the native faunal value (28.8% to 34.9%). The greater differentiation of aquatic ecoregion fish faunas in B.C. was also reflected in faunal turnover, which increased from an average of 51.3% to 54.6% after incorporating nonnative species and extinctions or extirpations (matrix randomization test, $P < 0.005$). The influence of nonnative species and extirpations was detectable in the interrelationships among ecoregions (Fig. 3). For instance, bootstrap support for a tight relationship between Vancouver Island and the QCI dropped from 100% to 93% and the branch length between them increased in the total faunal tree (Fig. 3*b*). In addition, the bootstrap support for a Yukon and Columbia ecoregion group dropped from 62% to under 50% and the bootstrap support for a linking of Columbia, Yukon, and Mackenzie ecoregions dropped from 66% to 57%. Finally, the Fraser ecoregion total fauna became more distinctly separate from the Central Coast ecoregion (which grouped with the North Coast ecoregion) in the NJ tree relative to the native faunal interrelationship.

At the family level, centrarchid fishes (sunfishes and basses) were the most widely introduced taxon, accounting for nine region introductions (a combination of four different species is nonnative in up to three ecoregions each). The single most widely introduced species was the brook trout (*Salvelinus fontinalis*); it has been introduced from east of the Rocky Mountains to four of B.C.'s eight aquatic ecoregions.

Comparisons among Canada-wide fish faunas

Historically, there was an estimated 197 native freshwater fishes in Canada; Ontario had the highest number (131 species) and Prince Edward Island the lowest (23 species) (Table 3). There are 48 species nonnative to Canadian freshwaters in at least one province or territory (including 21 from countries other than Canada), and four species have been declared extinct. Several nonnative species are recorded from two or more provinces or territories, and four species have been declared extirpated in more than one region. Consequently, there have been a total of 102 records of nonnative species and eight extinctions and extirpations among the 13 provinces and territories. Accounting for all nonnative species and extinction or extirpation events, Ontario still has the largest number of species (154), and Prince Edward Island, the fewest (23). Ontario has recorded the greatest number of nonnative species (28) and extinctions or extirpations (5); only Prince Edward Island has also recorded extirpations (3). Two of the territories (Yukon and Nunavut) have no recorded nonnative species (Table 3).

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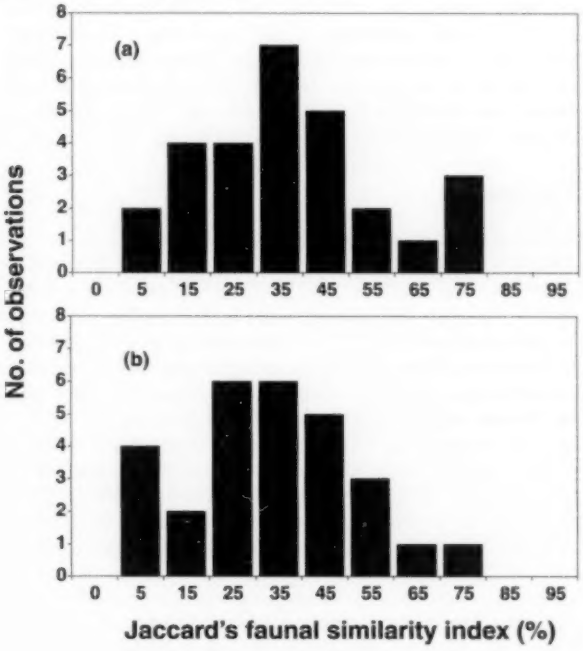
Table 2. Jaccard's faunal similarity coefficients for native (lower diagonal) and total (native + nonnative – extinctions or extirpations, upper diagonal) freshwater fish faunas among eight British Columbia aquatic ecoregions estimated from species presence–absence data.

	VanI	Fraser	Columbia	Mackenzie	Yukon	NorthC	QCI	CentralC
VanI	—	0.382	0.201	0.117	0.053	0.350	0.519	0.368
Fraser	0.357	—	0.492	0.338	0.172	0.491	0.269	0.615
Columbia	0.132	0.551	—	0.349	0.184	0.220	0.057	0.276
Mackenzie	0.120	0.350	0.288	—	0.283	0.306	0.096	0.339
Yukon	0.066	0.213	0.194	0.302	—	0.394	0.071	0.231
NorthC	0.452	0.591	0.244	0.327	0.406	—	0.467	0.722
QCI	0.765	0.341	0.108	0.102	0.071	0.483	—	0.438
CentralC	0.469	0.756	0.349	0.356	0.237	0.714	0.452	—

Note: VanI, Vancouver Island; Fraser, Fraser River; Columbia, Columbia River; Mackenzie, Mackenzie River; Yukon, Yukon River; NorthC, North Coast; QCI, Queen Charlotte Islands; CentralC, Central Coast.

Fig. 2. Frequency histogram of Jaccard's pairwise faunal similarity coefficients among eight British Columbia aquatic ecoregions for (*a*) native fish faunas and (*b*) total (native + nonnative – extinctions or extirpations) fish faunas.



Pairwise Jaccard's similarity matrices of native faunas averaged 27.1%, ranging from a low of 3.8–4.4% between Yukon and Northwest Territories, respectively, and Prince Edward Island to a high of 70.0% between Saskatchewan and Manitoba (Table 4). Clustering these coefficients resolved three groupings of regions: a "northwestern region" consisting of the three territories, B.C., and Alberta; a "central region" consisting of Saskatchewan through Quebec; and an "eastern region" consisting of New Brunswick, Nova Scotia, Prince Edward Island, and Newfoundland/Labrador (Fig. 5*a*). Pairwise faunal turnover between native faunas averaged 59.9%, ranging from 17.6% between Saskatchewan and Manitoba to 92.6% between Yukon and Prince Edward Island. After accounting for nonnative species and extinctions or extirpations in Canadian freshwater fish faunas, similarities averaged 28.3%, ranging from a low of 5.9–7.5% between Yukon and Northwest Territories, respectively, and Prince Edward Island to a high of 65.3–66.7% between Saskatchewan and Manitoba and New Brunswick and Nova Scotia, respectively (Table 4). Clustering these similarity coefficients resolved the same general relationships as the native faunas. The only major differences included the tighter clustering of Nova Scotia and New Brunswick (87% bootstrap support; three shared introductions) separate from Prince Edward Island and Newfoundland/Labrador, within the eastern faunal region (Fig. 5*b*). In addition, bootstrap support for a northwestern grouping (Nunavut, Yukon, and Northwest Territories, B.C., and Alberta) declined from 63% in the native faunas to less than 50% in the total faunas. There was also a slight decline in the total branch length separating the northwestern grouping from the central grouping (i.e., Saskatchewan through Quebec; Figs. 5*a*, 5*b*).

Over all pairwise comparisons, the difference between the mean native and total faunal pairwise Jaccard's coefficient matrices was small but highly significant (27.1% similarity versus 28.3%, respectively, matrix randomization test, $P = 0.009$; Fig. 6). As a further index of homogenization, mean pairwise faunal turnover dropped an average of 1.8% from 59.9% to 58.1% (matrix randomization test, $P = 0.0004$), but pairwise variation was considerable. For instance, there was a gain in turnover between Nova Scotia and Prince Edward Island from 28.6% to 39.7%, but turnover declined between B.C. and Quebec from 69.3% to 54.9% after incorporating nonnative species and extinctions or extirpations.

The B.C. freshwater fish fauna showed the greatest change in faunal similarity, with an average increase in Jaccard's similarity index of 4.9% (or an average 25.1% of the native faunal value) (Fig. 7). British Columbia's fish fauna became more similar to the faunas of all areas except the three territories, where Jaccard's similarity actually dropped an average of 5.6% (or 14.7% of the native faunal value). The greatest increase in similarity observed in comparisons with B.C. freshwater fish fauna was that with Quebec (11.0%), Nova Scotia, Ontario, and Manitoba (8.4–8.6% each). Among all regions, the largest proportional homogenization occurred between B.C. and Quebec (86.7% of native value), Alberta and Prince Edward Island (82.1%), B.C. and Nova Scotia (77.3%), Saskatchewan and Prince Edward Island (69.0%), and Yukon Territory and New Brunswick (64.1%).

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Fig. 3. Relationships among eight aquatic ecoregions of British Columbia. Relationships are depicted as a neighbor-joining tree obtained by clustering pairwise values of 1.0 – Jaccard's faunal similarity coefficients for (*a*) native faunas and (*b*) total faunas (native + nonnative – extinctions or extirpations). Wagner parsimony analyses resolved the same topology as neighbor-joining clustering, and the numbers at branch points represent bootstrap support levels from 100 replicate parsimony analyses of the species presence–absence matrix. The scale bar represents 0.1 unit of 1.0 – Jaccard's faunal similarity coefficient. VanI, Vancouver Island; Fraser, Fraser River; Columbia, Columbia River; Mackenzie, Mackenzie River; Yukon, Yukon River; NorthC, North Coast; QCI, Queen Charlotte Islands; CentralC, Central Coast.

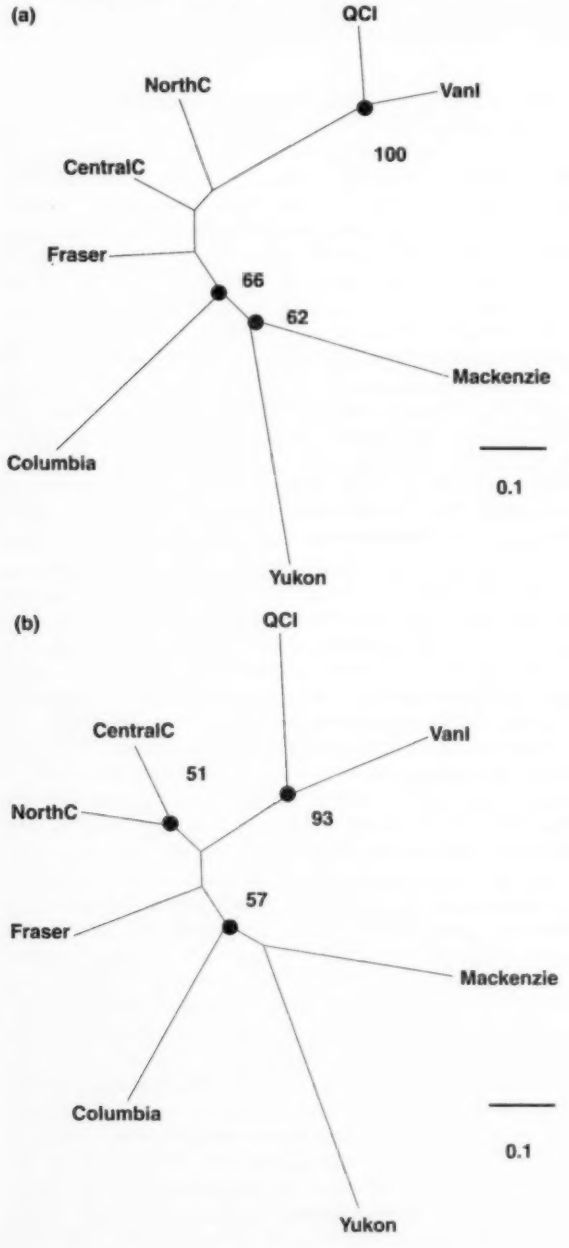
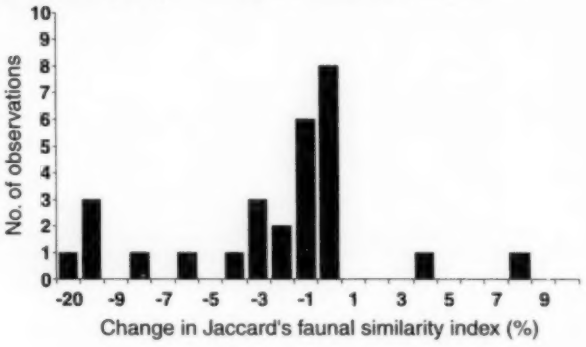


Fig. 4. Frequency histogram of the percentage change in pairwise Jaccard's faunal similarity coefficients between native and total (native + nonnative – extinctions or extirpations) freshwater fish faunas for eight aquatic ecoregions of British Columbia.



In the case of Alberta and Prince Edward Island, these two provinces went from having four species in common to having eight species in common. The largest percentage decrease in faunal similarity (55.6% to 43.2%, –22.3% from native value) occurred between Nova Scotia and Prince Edward Island, which resulted from three extirpations of shared native fauna in Prince Edward Island and six nonnative species now found in one or the other province.

Discussion

Faunal similarity and geographic scale

Natural levels and patterns of biodiversity of freshwater faunas worldwide are at risk of deterioration from anthropogenic activities and homogenization (the tendency for faunas to become more similar to one another over time) from the combined effects of species introductions and extinctions or extirpations. The flip side of homogenization, when faunas become more divergent from these same human activities, I have termed faunal differentiation. The present analysis has demonstrated both homogenization and differentiation in freshwater fish faunas at different geographic scales. For instance, aquatic ecoegions within B.C. have, by an average of 3.5%, become significantly less similar to one another as a result of including nonnative species and extinctions or extirpations in calculations of Jaccard's similarity coefficients and faunal turnover between ecoregions. On the other hand, comparisons between specific ecoregions indicated that some homogenization has clearly occurred (e.g., the Vancouver Island and the Columbia River ecoregions increased in similarity by 7%). At the largest geographic scale across Canada, on average, faunas have become significantly more similar by only about 1.2%, but some areas such as B.C. showed greater levels of homogenization.

The apparent dependence of homogenization and differentiation on spatial scale is probably best explained by the differing patterns of nonnative species occurrence. For instance, B.C. ecoregions have become more differentiated owing to the apparently idiosyncratic nature of most fish introductions in B.C. Of the 21 freshwater fishes nonnative to B.C., only five (brook trout (*Salvelinus fontinalis*), common carp (*Cyprinus carpio*), American shad (*Alosa sapidissima*), goldfish (*Carrasius auratus*), and brown bullhead (*Ameiurus nebulosus*))

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Table 3. Numbers of native, nonnative, and total freshwater fish species in the 13 provinces and territories of Canada.

Region	No. of historical native species	No. of extant nonnative species	No. of extirpated species	Total no. of extant species
Yukon Territory	31	0	0	31
Northwest Territories	48	1	0	49
Nunavut Territory	25	0	0	25
British Columbia	67	15	0	82
Alberta	52	11	0	63
Saskatchewan	59	9	0	68
Manitoba	77	12	0	89
Ontario	131	28	5[a]	154
Quebec	102	8	0	113
New Brunswick	45	5	0	50
Nova Scotia	33	7	0	40
Prince Edward Island	23	3	3	23
Newfoundland/Labrador	25	3	0	28

Note: The total number of extant species is equal to the total number of historical native species minus any extinctions or extirpations, plus nonnative species. The table was assembled from data found in the Wild Species 2000 database (http://www.wildspecies.ca).

[a]Includes four species endemic to Ontario (= extinctions).

Table 4. Jaccard's faunal similarity coefficients for native (lower diagonal) and total (native + nonnative – extinctions or extirpations, upper diagonal) freshwater fish faunas among 13 provinces and territories of Canada estimated from species presence–absence data.

	YT	NWT	NUT	BC	ALTA	SASK	MAN	ONT	QUE	NB	NS	PEI	NFLD/LAB
YT	—	0.600	0.514	0.329	0.306	0.207	0.176	0.128	0.143	0.141	0.109	0.059	0.229
NWT	0.580	—	0.480	0.401	0.436	0.345	0.302	0.216	0.246	0.207	0.141	0.075	0.203
NUT	0.514	0.490	—	0.244	0.275	0.224	0.200	0.119	0.150	0.190	0.102	0.091	0.262
BC	0.400	0.456	0.296	—	0.465	0.339	0.326	0.242	0.291	0.234	0.184	0.082	0.183
ALTA	0.317	0.449	0.283	0.469	—	0.523	0.434	0.269	0.304	0.215	0.144	0.103	0.197
SASK	0.216	0.372	0.254	0.273	0.563	—	0.653	0.396	0.448	0.297	0.213	0.110	0.185
MAN	0.174	0.316	0.229	0.241	0.433	0.700	—	0.528	0.566	0.311	0.206	0.120	0.182
ONT	0.102	0.193	0.130	0.158	0.253	0.397	0.529	—	0.628	0.248	0.190	0.106	0.145
QUE	0.118	0.230	0.165	0.182	0.294	0.425	0.543	0.641	—	0.405	0.319	0.183	0.248
NB	0.134	0.208	0.207	0.155	0.183	0.268	0.298	0.231	0.400	—	0.667	0.404	0.529
NS	0.067	0.110	0.115	0.099	0.104	0.179	0.183	0.155	0.285	0.660	—	0.432	0.417
PEI	0.038	0.044	0.067	0.047	0.056	0.069	0.087	0.085	0.202	0.445	0.555	—	0.457
NFLD/LAB	0.191	0.177	0.250	0.136	0.149	0.135	0.159	0.130	0.245	0.522	0.415	0.500	—

Note: YT, Yukon Territory; NWT, Northwest Territories; NUT, Nunavut Territory; BC, British Columbia; ALTA, Alberta; SASK, Saskatchewan; MAN, Manitoba; ONT, Ontario; QUE, Quebec; NB, New Brunswick; NS, Nova Scotia; PEI, Prince Edward Island; NFLD/LAB, Newfoundland and Labrador.

have been introduced (or spread) to three or more ecoregions. In addition, the brook trout is the only species that is nonnative to as many as four ecoregions. There are also four species of fishes that are native to B.C. but that have been introduced or have spread to particular B.C. ecoregions in which they were historically absent: lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), Arctic grayling (*Thymallus arcticus*), walleye (*Stizostedion vitreum*), and westslope cutthroat trout (*Oncorhynchus clarki lewisi*), but none is now found in more than one new ecoregion. Consequently, the relatively limited number of introductions to multiple ecoregions has likely promoted differentiation of B.C. freshwater fish faunas rather than homogenization.

By contrast, the situation in Canada as a whole indicated a much more general trend towards homogenization, with 50 of 78 (64%) pairwise comparisons showing increasing similarity among regions. In fact, if comparisons involving the three territories are removed, 33 of 45 pairwise comparisons (73%) result in increased Jaccard's coefficients. The homogenization of the Canadian fauna is driven largely by a few species that have been introduced widely. There are, for instance, 12 species that have been introduced to three or more regions and four species (goldfish, rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), and smallmouth bass (*Micropterus dolomieu*)) that have been introduced to six or more of the 13 provinces or territories. Marchetti et al. (2001) also showed that the degree of homogenization in California freshwater fishes depended on spatial scale. At the smallest scale examined, that of individual watersheds, homogenization was minimal and there was evidence of faunal differentiation between some watersheds. By contrast, at the largest spatial scale examined, that of zoogeographic provinces (analogous to the B.C. ecoregions), there was clear evidence of faunal homogenization and loss of beta diversity. Similar to the proposed explanations for differing pat-

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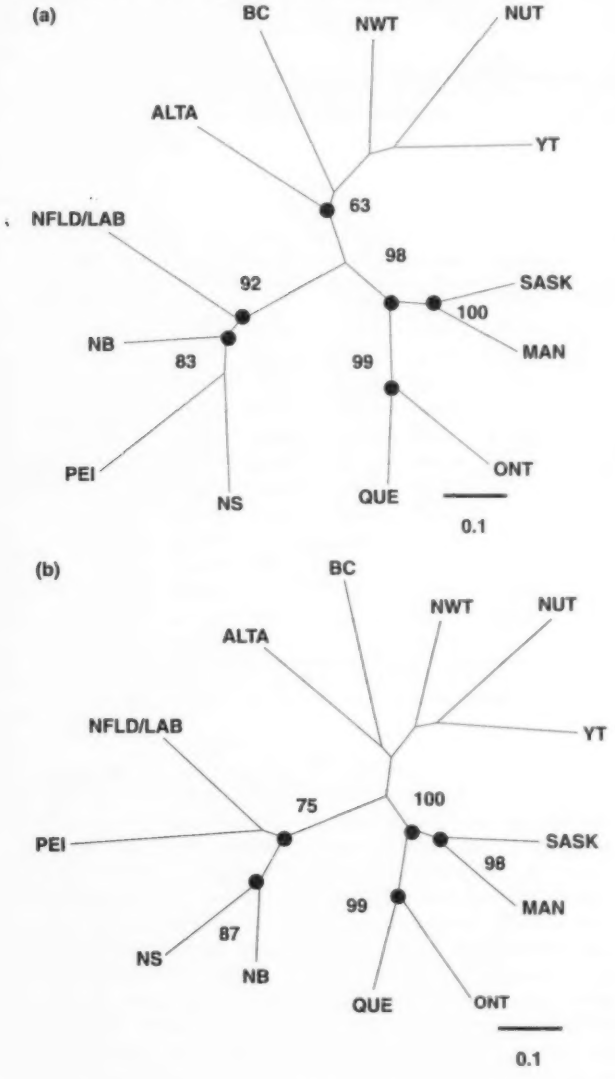
Fig. 5. Relationships among 13 provinces and territories of Canada. Relationships are depicted as a neighbor-joining tree obtained by clustering pairwise values of 1.0 – Jaccard's faunal similarity coefficients for (*a*) native faunas and (*b*) total (native + nonnative – extinctions or extirpations). Wagner parsimony analyses resolved the same topology as neighbor-joining clustering, and the numbers at branch points represent bootstrap support levels from 100 replicate parsimony analyses of the species presence–absence matrix. The scale bar represents 0.1 unit of 1.0 – Jaccard's faunal similarity coefficient. YT, Yukon Territory; NWT, Northwest Territories; NUT, Nunavut Territory; BC, British Columbia; ALTA, Alberta; SASK, Saskatchewan; MAN, Manitoba; ONT, Ontario; QUE, Quebec; NB, New Brunswick; NS, Nova Scotia; PEI, Prince Edward Island; NFLD/LAB, Newfoundland and Labrador.



terns within B.C. and across Canada, Marchetti et al. (2001) suggested that faunal differentiation at small spatial scales was due to the haphazard nature of fish introductions among individual watersheds, whereas homogenization at larger scales was due to greater commonality in the taxonomic composition of nonnative species. These similar observations in independent studies highlight the importance of considering spatial scale in assessments of faunal homogenization and differentiation in conservation.

Losses of native fauna can also clearly play a role in homogenization, but they cannot explain the homogenization resolved here. For instance, introductions have been much more common than extinctions or extirpation in terms of

Fig. 6. Frequency histogram of Jaccard's pairwise faunal similarity coefficients among 13 provinces and territories of Canada for (*a*) native fish faunas and (*b*) total (native + nonnative – extinctions or extirpations) fish faunas.

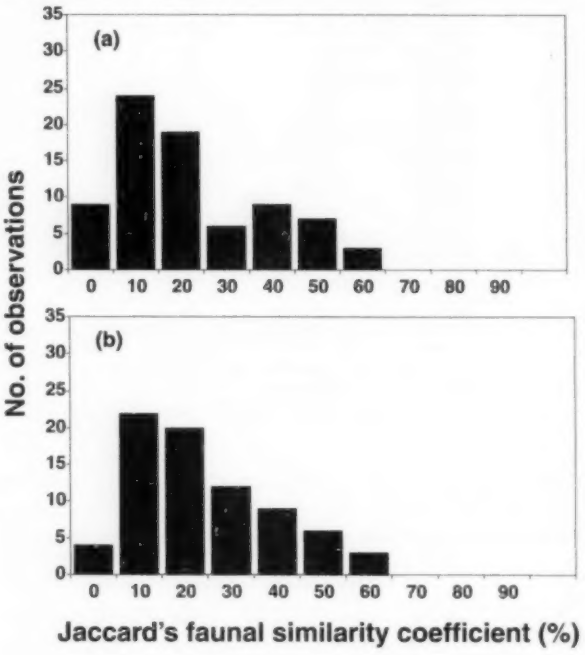
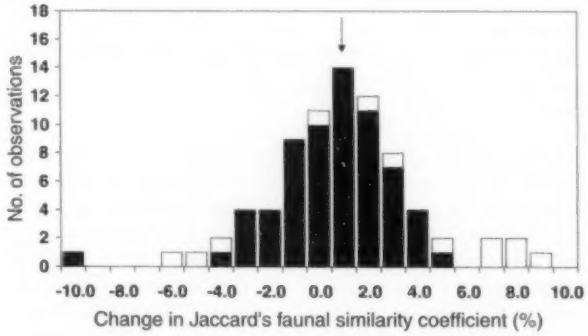


Fig. 7. Frequency histogram of the percentage change in pairwise Jaccard's faunal similarity coefficients between native and total (native + nonnative – extinctions or extirpations) freshwater fish faunas for 13 provinces and territories of Canada. Open bars are for comparisons involving British Columbia. The arrow represents the mean difference between all 78 pairwise comparisons of native and total Jaccard's coefficients.



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both the number of events and their geographic scope. There have been only eight recorded extinctions or extirpations in Canada with most (5) occurring in Ontario and the rest (3) confined to a single other province, Prince Edward Island. Nevertheless, within specific comparisons, extinctions and extirpations have been important factors in homogenization. For instance, for a variety of reasons, including predation by introduced sea lamprey (*Petromyzon marinus*), the native salmonid fauna of the Great Lakes region of Ontario was decimated, including the extinction of several species of endemic whitefishes, *Coregonus* (see Smith 1980). The extinction or extirpation of much of the Great Lakes salmonid fauna precipitated a program of introductions of salmonid fishes from Canada's west coast (e.g., coho (*Oncorhynchus kisutch*) and chinook salmon and rainbow trout) to rehabilitate the sport fishery (Bureau of Sport Fisheries and Wildlife 1973). This combination of extinctions of fishes endemic to Ontario, introductions of native B.C. fishes to Ontario, as well as introductions to B.C. of fishes found in Ontario (e.g., brook trout, various centrarchids, and two catfishes) has clearly made the faunas of these two areas more similar. Rahel (2000) also found that introductions, rather than extinctions or extirpations, caused homogenization of the U.S. freshwater fish fauna.

Comparative analysis of homogenization

The pattern of homogenization across Canada is similar to the pattern reported by Rahel (2000) for U.S. continental freshwaters, but the mean increase in Jaccard's similarity in Canada was considerably lower (1.2% versus 7.2%). The evidence for lower homogenization in Canadian freshwater fishes occurs even though Canada has a much lower diversity of native species than the U.S. (with an estimated 800 native species versus 197 in Canada) and a similar rate of introductions should have a greater effect in Canada. In fact, there have been proportionally more introduction events in the U.S. than in Canada. Rahel (2000) reported 901 introduction events in the U.S. across 48 states or an average of 18.8 events per state, whereas in Canada there have been only 102 across the 13 provinces and territories or an average of 7.8 introduction events. In addition, extinctions and extirpations have been more common in the U.S.; Rahel (2000) reported 196 extinction or extirpation events (4.1 per state), whereas there have been only eight in Canada (0.62 per province or territory). Both the greater rate of introductions and extinctions or extirpations in the U.S. should promote greater homogenization of freshwater fish faunas. A possible instigating factor in the greater rate of homogenization in U.S. freshwaters is the fact that management of freshwater fisheries are subdivided into 48 distinct jurisdictional units (i.e., state fish and game departments) vs. only 13 in Canada (provincial and territorial governments). Consequently, there are many more potential pairwise interactions (1128 vs. 78, respectively) and potentially different management attitudes among states that could lead to introduction or extinction or extirpation events.

The evidence for faunal differentiation in B.C. and homogenization across Canada is generated by sets of commonly introduced species that are remarkably similar to each other and to fish species that dominate introductions in the U.S. In fact, the top five species introduced in Canada (common carp, brown trout, goldfish, rainbow tout, and smallmouth bass) are the same as in the U.S. (Rahel 2000). Further, with the exception of the striped bass (*Morone saxatilis*), the top 17 species introduced in the U.S. have all been introduced to at least one region in Canada as well (Rahel 2000). Most of these commonly introduced species across Canada and the U.S. have also been introduced into B.C., but only a few (common carp, goldfish, brown bullhead, American shad, and brook trout) have been introduced to more than two ecoregions. This reflects the more haphazard pattern of introductions in B.C. and contributes to the differentiation of faunas within B.C.

These commonly introduced freshwater fishes also reflect the important and common motivating forces of introductions in Canada and the U.S. — for the purposes of recreational fishing (e.g., brown and rainbow trout, smallmouth bass) and aquaculture (rainbow trout, common carp) and by accidental releases from aquaria (e.g., goldfish). These pressures have, however, resulted in greater average changes to the fish faunas of the U.S. than Canada. In the former, 17 states have over 25% of their contemporary fish faunas consisting of introduced species (and three are over 50%), whereas Ontario, B.C., Alberta, and Nova Scotia have the highest proportions of nonnative faunas (all from 21–22%) and the average across Canada is "only" 12.5 (standard deviation (SD) = 6.5%).

Consequences of faunal change

Several issues should be considered in light of the current analysis of differentiation and homogenization in Canadian freshwater fish faunas. First, the primary data consist of presence–absence information only and, consequently, do not take relative abundance into account in calculating faunal similarity. Although such measures are available for smaller scale analyses of biodiversity (e.g., within individual lakes or river reaches), the number of individuals of each fish species across broad geographic regions cannot generally be determined. An alternative may be to record presence or absence of populations within individual water bodies or major drainages to produce more detailed estimates of faunal diversity within provinces and territories. The collection of data by ecoregion for B.C. (McPhail and Carveth 1994) is a step in this direction and more detailed "extent of occurrence" measures are needed for more biologically realistic assessments of faunal homogenization. A further refinement may be to extend the approach adopted by McPhail and Carveth (1994) to include faunal surveys for aquatic ecoregions that transcend political boundaries and better reflect the natural faunal boundaries for all of Canada. There is a current attempt to define a workable number of aquatic ecoregions for all of Canada (N. Mandrak, Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans Canada, P.O. Box 5050, 867 Lakeshore Road, Burlington, ON L7R 4A6, personal communication), and this may form the basis for assessments of homogenization and differentiation for natural aquatic groups.

Second, the current analysis neglects faunal homogenization and differentiation within ecoregions. Again, this is largely an issue of current limitations on data collection and analysis. For instance, rainbow trout have been introduced among multiple watersheds within individual ecoregions in

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B.C., and this results in some level of homogenization (or differentiation) on very small scales that can have the same consequences as at the level of aquatic ecoregions within the province as a whole (e.g., see Scott and Helfman 2001). Third, analyses of homogenization and differentiation reflect the situation at a particular time only, and updates should be regularly performed. For instance, increases in nonnative species via introductions, transplants, and invasions may result in short-term increases in biodiversity in the narrow sense (i.e., there are more species in a particular place). The eventual consequences of introductions, however, may result in lowered native biodiversity if the extinction process runs its course and nonnative species replace native species (Scott and Helfman 2001). This process may result from a "relaxation" of species diversity, raised artificially by human activities, towards levels before human-induced changes. Because many introduced species are either chosen for their broad environmental tolerances or are the "survivors" from accidental introductions, such faunal relaxation could result in a subset of widely distributed species increasing homogenization, and reducing biodiversity, over the longer term (Rahel 2002). Such faunal relaxation may become common in the future because intentional introductions are no longer permitted or are discouraged in most Canadian jurisdictions. In addition, virtually all of Canada's freshwater fish fauna is postglacial in origin. Consequently, species diversity in postglacial environments may not be at equilibrium levels and, over the short term, may be able to "absorb" introduced species resulting in short-term increases in biodiversity (Brown and Lomolino 1998; Rahel 2002). Two issues, however, argue that the apparent benefits of such increased biodiversity are illusionary. First, it is difficult to predict the eventual outcome of introductions on native fauna, and if introductions result in the extinction of endemic fauna, then no matter how much total biodiversity has increased, the loss of endemics results in permanent losses of biodiversity worldwide. Second, both homogenization and differentiation from the combined effects of introductions and extinctions or extirpations may result in altered faunal and zoogeographic "relationships" among watersheds and larger geographic units (e.g., the relative similarities among areas). The major grouping of provinces and territories into northwestern, central, and eastern faunal regions likely reflects the postglacial recolonization of constituent provinces and territories from distinct sets of Wisconsinan glacial refugia. The northwestern grouping was predominantly recolonized from the Bering, Pacific, and Mississippi refugia, the central grouping from the Bering, Mississippi, and Atlantic refugia, and the eastern grouping was predominantly colonized from the Mississippi, Atlantic, and Acadian refugia (McPhail and Lindsey 1970; Schmidt 1986; Scott and Crossman 1998). Such relationships are part of the faunal legacy of Canada and are of inherent and perhaps under appreciated conservation value. My analyses, both for B.C. and for Canada as a whole, revealed slight but detectable changes in ecoregion interrelationships of native faunas after accounting for nonnative species and extirpations or extinctions. The changes in relationships reflect relatively minor rearrangements of component groups nested within larger regional units (e.g., relative position of the Columbia ecoregion within the Mackenzie–Yukon–Columbia grouping in B.C., the position of P.E.I. within the eastern grouping of provinces) and degrees of differentiation among faunal groups. Both the kinds and magnitudes of these topological changes are consistent with the relatively small but significant changes in Jaccard's indices between native and total faunas. Although the detected changes were small, the NJ analyses provide a necessary baseline and a convenient method to visualize changes in regional relationships in the future. Finally, the differentiation and homogenization of diversity can also occur in terms of within-species genetic diversity. This topic has received considerable attention in terms of its relevance to within-species biodiversity conservation in fishes (e.g., Hindar et al. 1991; Ryman et al. 1995), but large-scale geographic studies of anthropogenic-based genetic differentiation or homogenization are lacking for the relevant Canadian fishes (e.g., salmonid fishes subject to hatchery or aquacultural production; cf. Reisenbichler et al. 1989).

In conclusion, Rahel (2002) outlined several steps to help reduce the rate of biotic homogenization: reducing or eliminating intentional and accidental introductions, reducing the rate of native species extinctions or extirpations, reducing habitat changes that result in abiotic homogenization which indirectly promotes biotic homogenization, and rehabilitating native faunas through exotic species removal. The results of studies such as the current analyses can hopefully also contribute by establishing a baseline to help track future changes in faunal composition and ecoregion relationships in B.C. and in Canada as a whole.

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Test fishery indices for sockeye salmon (*Oncorhynchus nerka*) as affected by age composition and environmental variables

Lucy Flynn and Ray Hilborn

Abstract: In this paper, we explore sources of variability in test fishing indices for sockeye salmon (*Oncorhynchus nerka*) and illustrate potential solutions. For our analysis, we use the Port Moller test fishery in Bristol Bay, Alaska. The traditional model used to forecast run size using Port Moller test fishery data is based on a simple linear regression of total returns to the fishing districts against the cumulative test fishery catch-per-unit-effort (CPUE) index on a given date. We show that much of the inaccuracy of recent forecasts based on test fishery indices is due to the variable age composition of sockeye runs and the unequal vulnerability of respective age classes to the test fishing gear. We also illustrate solutions to the problems presented by variability in migration route and variability in return timing. In warmer years, we found that there was an increase in effective vulnerability to the test fishing gear and that the strength of this relationship increased linearly with the average body length of age classes. Retrospective analysis shows that correcting for age composition, migration route, and timing provides an in-season index of abundance with an average error of 6.7 million fish or 21%, compared with 33% for previous models.

Résumé : Notre étude examine les sources de la variabilité dans les indices de pêche expérimentale du saumon rouge (*Oncorhynchus nerka*) et illustre des solutions potentielles au moyen d'une analyse de la pêche expérimentale de Port Moller dans la baie de Bristol, Alaska. Le modèle couramment utilisé pour prédire la taille de la montaison à partir des données de la pêche expérimentale de Port Moller est basé sur une régression linéaire simple des rendements totaux des districts de pêche sur l'indice de capture cumulative totale de la pêche expérimentale par unité d'effort (CPUE) à une date donnée. Nous démontrons qu'une partie importante de l'inexactitude des prévisions récentes basées sur les indices de pêche expérimentale est due à la composition en âge variable de la montaison de saumons rouges et de la vulnérabilité inégale des différentes classes d'âge aux engins de pêche expérimentale. Nous décrivons aussi des solutions aux problèmes posés par la variabilité de la route de migration et de la chronologie des retours. Les années plus chaudes, il y a une augmentation de la vulnérabilité effective aux engins de pêche et la force de cette relation augmente de façon linéaire avec la longueur moyenne du corps des classes d'âge. Une analyse rétrospective montre que des corrections pour tenir compte de la composition en âge, la route de migration et le moment de la migration permettent l'élaboration d'un indice d'abondance intra-saisonnier avec une marge d'erreur moyenne de 6,7 millions de poissons ou de 21 %, au lieu de 33 % chez les modèles antérieurs.

[Traduit par la Rédaction]

Introduction

Reliable salmon forecasts are one of the main objectives of salmon research; they are needed not only for salmon harvest management and conservation of stocks, but also for the efficient operation of salmon fisheries and processing industries (Ishida et al. 2000). Although preseason run size forecasts are available and provide some indication of eventual run strength, run size estimates are adjusted in-season as indicators of actual run size emerge (Fried and Hilborn 1988). Test fishing, whether outside fishing areas for an in-season run size estimate, in fishing areas for an estimate of fish buildup in those areas, or in rivers for an estimate of recent escapement, is often used to update knowledge regarding run size during the fishing season.

The assumption implicit in the use of test fishing indices is that of a proportional relationship between the catch-per-unit-effort (CPUE) of the test gear and actual abundance. One way to quantify this relationship is to calculate the return-per-index (RPI) point, the actual number of fish present or expected per test fishery index point:

$$(1) \qquad \mathrm{RPI} = R/\mathrm{CPUE}$$

where R indicates the returning run size, number of fish in-river, or other value of interest.

Test fisheries for salmon have historically yielded substantial variability in RPI values. For example, Cox-Rogers and Jantz (1993) reported annual average RPI values ranging from 426 to 1254 (approximately threefold variability) for the Skeena River sockeye salmon (*Oncorhynchus nerka*) gillnet test fishery between 1970 and 1992. The researchers

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defined two categories of factors influencing RPI, those affecting vulnerability and those affecting accessibility. Key factors affecting the vulnerability of fish to the test fishing gear are size selectivity and gear saturation, whereas those affecting accessibility in an in-river test fishery may include river hydrology or drift topography (Cox-Rogers and Jantz 1993). In a marine environment, accessibility may logically be affected by temperature, salinity, ocean currents, or other factors influencing migratory behavior. These conditions may influence accessibility by acting on migration timing, speed, or path, on swimming depth, or on some combination of variables.

Size selectivity presents an obstacle because the size distribution of many returning runs is highly variable, mainly because of the variability in relative age class components. Westrheim (1998) reported that the Fraser River chinook salmon (*Oncorhynchus tshawytscha*) test fishery, regardless of the age composition of the returning chinook salmon run, consistently sampled fish of the same ages (depending on the mesh size used). Researchers concluded that mesh size selectivity introduced enough bias to make a single mesh size gillnet test fishery unreliable for estimating population sizes. Although the relationship between age, size, and vulnerability is well understood, most efforts to account for size selectivity in test fishing indices have simply concentrated on a measurement such as the mean length of fish in test catches. Cox-Rogers and Jantz (1993) calculated a Skeena River index adjusted for mean fish size, but resulting run size estimates were only significantly more accurate in one of four historical periods (Cox-Rogers and Jantz 1993, their table 10). The Alaska Department of Fish and Game (ADF&G) also used the average lengths of sockeye salmon caught in the Port Moller test fishery, which were used to forecast the run to Bristol Bay, Alaska, to estimate RPI values (e.g., Yuen 1980; Eggers and Fried 1984; Fried 1985). A review of methods used to interpret the Port Moller test fishing indices considered ocean age data for use in forecasting (Eggers and Fried 1984). Researchers estimated RPI from mean fish length for all age groups combined and for 2-ocean and 3-ocean fish (all fish that had spent 2 and 3 years at sea, respectively) separately but concluded that the ocean age based model was less accurate than that using pooled ocean age groups (Eggers and Fried 1984, their table 7). A literature search produced no reports of age composition being used in practice to interpret test fishery data.

Migration timing can have a substantial effect on in-season estimates of run size, because on a given day, substantially more or less of the run may have been available for observation than that of the historical average. For example, a high cumulative CPUE index may indicate a large run or a small but very early run, with no reliable way to distinguish between the possibilities. Fisheries for pink salmon (*Oncorhynchus gorbuscha*), the only Pacific salmon species that do not display variability in age at return, have been able to address this problem by monitoring sex ratios (Zheng and Mathisen 1998). Because male salmon return slightly earlier than females, the sex ratio of fishery catches is indicative of the position in time of the run relative to the 50% date (the date at which half of the run has passed and the sex ratio is equal). Unfortunately, salmon species with multiple age classes present confounding factors because each age or size class displays its own sex ratio on a given date.

Although no reliable indicator of run timing is available from test fishery data, a great deal of attention has been focused on the relationship between migration timing and environmental temperatures. Numerous studies have reported significant correlations between sea surface temperatures (SSTs) and salmon migration timing (i.e., Blackbourn 1987; Karlsson et al. 1994; Hodgson 2000). Several studies have also found significant correlations using air temperatures (Burgner 1980; Mundy 1982), citing that they are highly correlated with SSTs (Hofmeister 1994) and may be more accurate and more easily obtained (Burgner 1980). However, to our knowledge, the findings of no such study have been directly applied to the adjustment of in-season run size estimates.

Geographic shifts in migratory paths, whether across a larger geographic area or across a river width, are not as easily related to environmental variables. In at least one case, such a shift has been directly linked directly to one explanatory variable; Xie and Hsieh (1989) were able to predict the latitude of landfall and subsequent migration path of Fraser River sockeye salmon based on sea surface temperatures. However, in many cases, the causal mechanisms are not as well understood or as easily measured. For example, Bristol Bay sockeye salmon are believed to actively avoid low salinity water until they are near their home river (Straty 1975), and their migration route through the Aleutian islands (Fujii 1975) and along the northern side of the Alaskan Peninsula towards Bristol Bay is believed to be determined primarily by salinity conditions (D.E. Rogers, Box 355020, University of Washington, Seattle, WA 98195, personal communication). However, collecting comprehensive salinity data for the area in question is not economically feasible, and thus no direct relationship has been established. Furthermore, additional environmental variables such as surface currents (Favorite and Ingraham 1972) or temperatures may play an additional role in determining the exact migratory path and, therefore, confound any underlying relationship.

Recent years have seen management programs moving away from dependency on gillnet test fishing and towards alternative methods of estimation or enumeration. Although emerging methodologies may offer significant advantages over test fishing, each comes with its own sources of bias and challenges when interpreting data. For example, in 1992, a fishwheel project was begun on the Nass River in British Columbia with the suggestion that "fishwheels may provide a better index of abundance than the current gillnet test fishery because fishwheel catch rates do not appear to saturate at high fish abundance" (Link et al. 1996). However, researchers also reported that "the proportion of the total run captured in the fishwheels was higher early in the years during periods of very high sockeye abundance and high river flows than later when both fish abundance and water levels had declined" (Link et al. 1996), indicating that the alternative method did not eliminate variability in RPI. Many fisheries have established sonar programs to estimate or enumerate adult salmon population sizes. These sonar programs introduce a new suite of potential complicating factors, including species identification and variability in the number of fish

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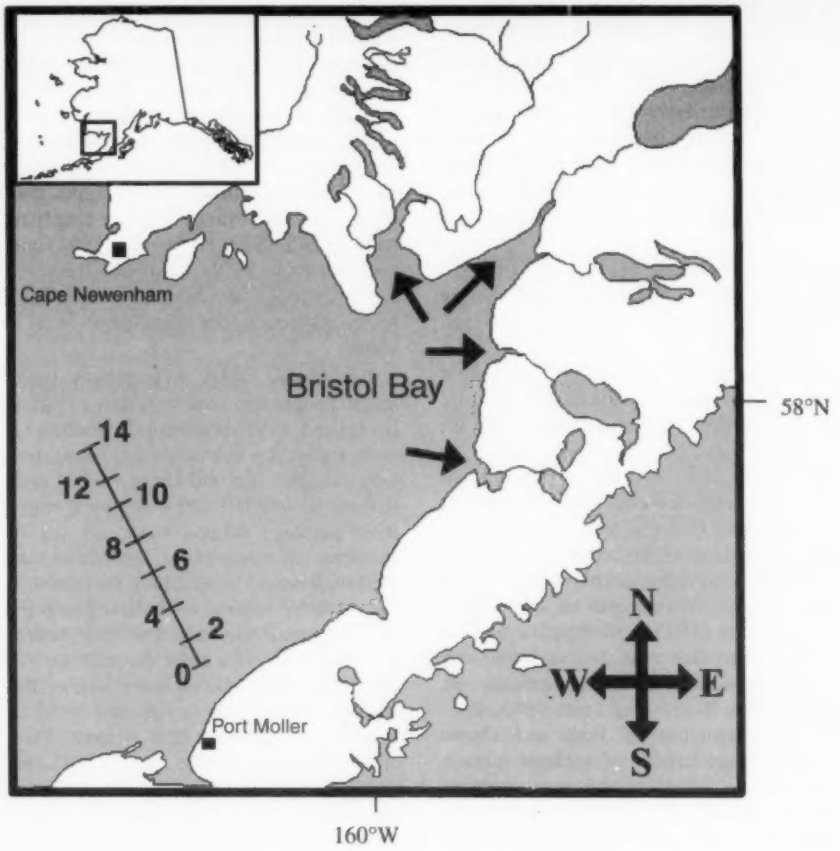
Fig. 1. Port Moller test fishery sampling stations and relative position of Bristol Bay commercial harvest districts in the state of Alaska, U.S.A. (inset). Sampling stations are numbered and principal commercial harvest areas are indicated with arrows.



avoiding the sampling gear (Romakkaniemi et al. 2000). Regardless of methodology, variability in RPI is likely to occur, and the more thorough our understanding of factors influencing CPUE in current test fisheries, the more prepared we will be to correctly interpret data generated by emerging methodologies.

In this paper, we explore sources of variability in CPUE with the goal of developing a refined method for forecasting run size with the information provided by the Port Moller test fishery. We begin our analysis by illustrating an adaptive sampling regime to account for geographic shifts in migration route. We examine the catches of each age class independently to account for unequal vulnerability to the test fishing gear and introduce a temperature factor to correct for temporal shifts in migration. We also examine the functional relationship of the prediction model and the appropriate level of model complexity. The examples provided in this analysis are applicable to any attempt to use sample catches for predicting runs or stock abundance.

Methods

The Port Moller test fishery

The Port Moller test fishery provides an in-season forecast of the sockeye salmon run to Bristol Bay, Alaska. The Port Moller test boat fishes at least four stations (designated stations 2, 4, 6, and 8) located along a transect line between Port Moller and Cape Newenham (Fig. 1) between 11 June and 10 July. Additional stations have been fished regularly in recent years (Rogers 2001). At each sampling station, a 200-fathom, 5⅛ inch (approximately 13.0 cm) mesh gillnet is fished for approximately 1 h. The station's CPUE index is calculated as the number of sockeye salmon caught per 100 fathoms per hour. A daily total CPUE index is calculated from these station indices. From the time that the Alaska Salmon Program took over the Port Moller test fishery in 1987 through 1995, the daily station indices from stations 2, 4, 6, and 8 were simply averaged (Rogers 2001). During 1995, catches were highest at station 8, leading researchers to believe that a significant portion of the run was traveling offshore from station 8. Beginning in 1996, the index was calculated according to the following formula, where the subscript i designates a given date:

$$(2) \qquad I_i = 0.8\,(I_{2i} + I_{4i} + I_{6i} + 2I_{8i})$$

and the multiplier 0.8 was used to change the previous years' indices as little as possible and create minimal confusion for the nonscientific audience. The above equation can be stated as "the daily index is proportional to the sum of the station indices 2–8, giving double weight to station 8 to account for

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Table 1. Actual returns to the fishery and predicted returns based on the traditional forecast model.

	Retrospective fits				Predictive fits		
Year	Return	Prediction	Error	% Error	Prediction	Error	% Error
1987	27.2	28.2	1.0	3			
1988	22.7	22.2	–0.5	–2			
1989	43.0	32.3	–10.7	–25			
1990	46.1	37.4	–8.7	–19			
1991	40.8	32.3	–8.5	–21			
1992	43.2	39.9	–3.3	–8			
1993	50.6	47.6	–3.0	–6			
1994	48.7	36.2	–12.5	–26			
1995	60.0	45.0	–15.0	–25			
1996	36.0	36.7	0.7	2			
1997	18.3	34.5	16.2	89	43.0	16.2	89
1998	17.9	26.9	9.0	50	38.2	9.0	50
1999	39.1	34.1	–5.0	–13	26.2	–5.0	–13
2000	23.3	21.0	–2.3	–10	36.9	–2.3	–10
2001	21.5	41.6	20.1	94	19.3	20.1	94
2002	17.0	39.4	22.4	131	44.0	22.4	131
Absolute average			8.7	33		12.5	65

Note: "Predictive fits" refers to predictions made using only data from years previous to that being predicted. We did not allow for the special cases of 1997 and 2000 in this fitting, so predictions subsequent to those years are not identical to those used in practice.

fish traveling further offshore" (Fig. 1). In years when the run is farther offshore, station 8 will have a higher proportion of the catches, and the total index will be inflated to account for the component of the run passing offshore from the sampling stations. Each daily index is added to the previous days' indices for a cumulative index. The subscript i is used to designate date for daily indices, and the subscript d is used to designate date for cumulative indices.

$$C_d = \sum_{i=1}^{d} I_i \quad (3)$$

Each day, an updated forecast of run magnitude is calculated using the historical relationship between the cumulative index through that date and the total run size in Bristol Bay. The model takes the form

$$F_d = m_d C_d + b_d \quad (4)$$

where the forecast on a given date, F_d, is calculated by multiplying that date's cumulative index C_d by a day-specific factor m_d and adding a day-specific intercept b_d (Helton 1991). This method worked well from the time that the University of Washington Fisheries Research Institute – Alaska Salmon Program took over its operation in 1987 until the late 1990s (Table 1; Fig. 2*a*). However, during the past 6 years, the test fishery has experienced a significant decline in forecasting accuracy (Table 1; Fig. 2*b*). In response to recent anomalous events, several modifications have been made. The 1997 return was overforecast by more than 100% and has been omitted from the predicting relationship as an outlier attributed to El Niño conditions. During the year 2000, roughly 70% of the fish caught on the sampling transect were caught at station 10, which had not been fished in earlier years, so the 2000 index was calculated using the sum of indices from stations 2–10 (Rogers 2001). However, the traditional method failed again in 2001, with one of the highest cumulative indices on record and a relatively small return of 21.5 million fish.

Data collection

Returns to Bristol Bay are composed almost exclusively of four major age classes: 1.2, 2.2, 1.3, and 2.3 (age designations are according to the European system, where *a.b* indicates *a* years of freshwater residence after hatching followed by *b* years of ocean residence). A scale sample is collected from each fish aboard the Port Moller test fishing boat, and samples are flown every other day to King Salmon, Alaska, to be aged by ADF&G. Records of test fishing indices, age compositions, and body lengths were taken from a database maintained by the Alaska Salmon Program at the University of Washington. We illustrate the relative sizes of the fish of each age class (Fig. 3). Age composition data for all fish are available from 1987, 1989, and 1991–2001. Summaries of the age compositions of Port Moller catches during the years 1988 and 1990 were provided by Don Rogers (Box 355020, University of Washington, Seattle, WA 98195, personal communication). Although data from 1988 and 1990 are included in general comparisons (i.e., Figs. 4–9), daily age information is not available and thus they were excluded from the model selection exercise. The Alaska Department of Fish and Game provided returns to the fishery by age class.

Although we initially explored SSTs in the Aleutian Island area in the Bering Sea and along the Port Moller sampling transect, we found that the air temperatures in Cold Bay, Alaska, during the month of June contributed the most to our model and proceeded only with those. Burgner (1980) found the combination of Adak, Alaska, and Cold Bay, Alaska, air temperatures to be the best predictor of Bristol Bay run timing, but because of the closure of a military base, Adak information is no longer available. Air tempera-

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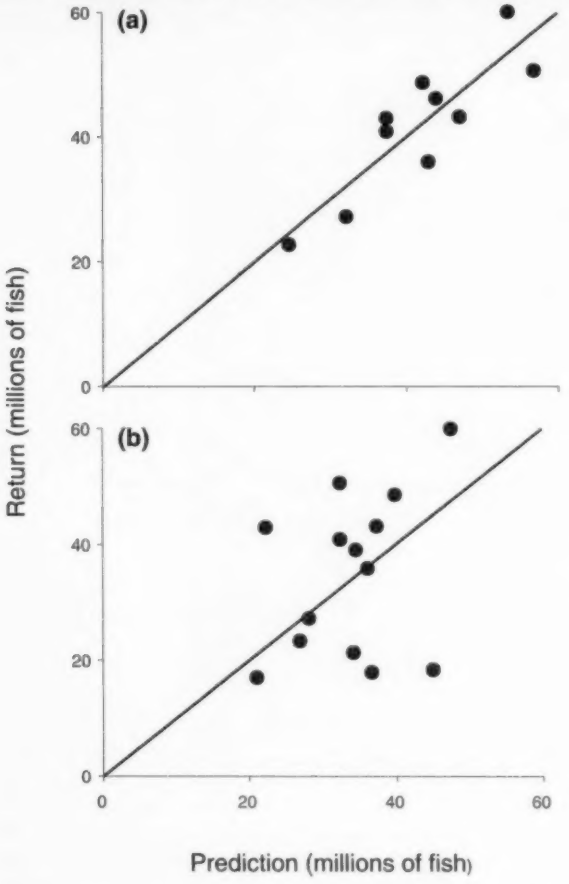
Fig. 2. Plots of the actual vs. predicted run sizes to Bristol Bay using the traditional forecasting method during the periods of (*a*) 1987–1996 and (*b*) 1987–2001. Lines illustrate a 1:1 ratio.



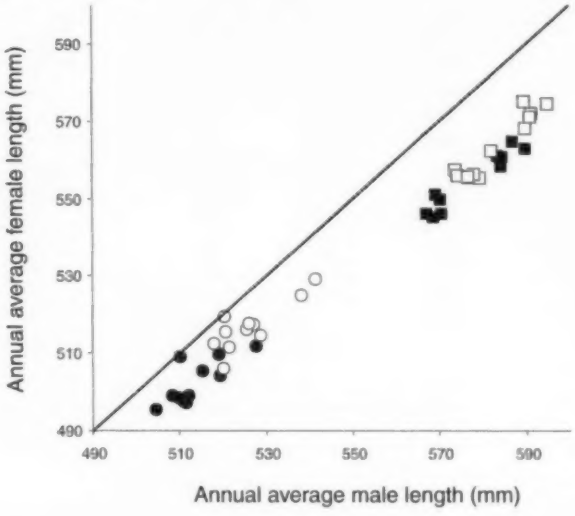
ture data from Cold Bay, Alaska, was provided by the National Climatic Data Center in Denver, Colorado (http://lwf.ncdc.noaa.gov/oa/ncdc.html).

Estimation of fish distribution

The following analysis can be performed for any day of the test fishing season (for notation and terms see Appendix A).

We first addressed the issue of the sockeyes' positions along the sampling transect. Although in recent years, the test fishing boat has moved offshore from station 8 to sample, for most years included in the data set, the sampling regime was limited to stations 2, 4, 6, and 8 (Fig. 1), making historical comparisons for additional stations impossible. We assumed fish density across the transect follows a normal distribution and hypothesized that the most appropriate method for estimating the index of abundance would be to calculate the area under this normal curve. The method has three logical advantages. (*i*) All fish are accounted for in years when a significant portion of the run crossed the transect northwest of station 8 without allowing for subjectively chosen special cases (i.e., 2000). (*ii*) The run is sampled appropriately both in years when the test fishery

Fig. 3. Annual average body lengths of Port Moller catches of the four major age classes during the past decade (1992–2001) for age 1.2 (●), age 2.2 (○), age 1.3 (■), and age 2.3 (□) sockeye salmon (*Oncorhynchus nerka*). Body length data were not available in electronic form for earlier years. The line illustrates a 1:1 ratio.



catches are concentrated tightly around a single station and in years when the catches are very spread out across the transect. (*iii*) Because historical data from stations 2–8 can also be used to estimate such an index, a change in sampling protocol does not lessen the amount of historical data available for comparison. Throughout the rest of this paper, we refer to the area under this estimated normal distribution as the "integral index".

The first step in calculating the cumulative integral index is to sum the daily station indices for cumulative station indices.

$$C_{xdy} = \sum_{i=1}^{d} I_{xiy} \quad (5)$$

Equation 5 can be stated as "the cumulative station x index on day d of year y is the sum of daily station x indices summed across the i days sampled since sampling day 1 of year y". (Subscript i denotes the day of a daily station index, and subscript d denotes the day of a cumulative station index.) Estimates of the mean location (μ_{dy}) and standard deviation (σ_{dy}) describing the location on the transect and of the scaling factor (S_{dy}) describing the magnitude of the cumulative test fishery indices on day d of year y are calculated by minimizing the difference between the observed and the predicted index for each location.

$$\hat{C}_{xdy} = S_{dy} \frac{1}{\sigma_{dy}\sqrt{2\pi}} \exp^{-\left(\frac{(x-\mu_{dy})^2}{2\sigma_{dy}^2}\right)} \quad (6)$$

Equation 6 can be stated as "the expected cumulative station x index on day d of year y is equal to the expected density of

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Table 2. Complete data set used in the analysis.

(*a*) Calculated cumulative indices, proportions of each age class, and interannual mean lengths.

	30 June cumulative index		30 June age proportions			
Year	Traditional	Integral	Age 1.2	Age 2.2	Age 1.3	Age 2.3
1987	956	2240	0.42	0.18	0.17	0.13
1988	523	1260	0.17	0.20	0.48	0.12
1989	1261	3281	0.10	0.20	0.35	0.18
1990	1632	3702	0.10	0.37	0.24	0.26
1991	1261	3332	0.11	0.56	0.14	0.14
1992	1812	7517	0.08	0.32	0.32	0.25
1993	2372	8173	0.04	0.20	0.25	0.49
1994	1538	4365	0.07	0.20	0.42	0.28
1995	2179	4320	0.14	0.15	0.51	0.19
1996	1580	3856	0.08	0.51	0.13	0.25
1997	1421	3076	0.09	0.33	0.26	0.26
1998	867	1911	0.19	0.38	0.08	0.33
1999	1392	3726	0.45	0.21	0.26	0.08
2000	435	4076	0.14	0.64	0.08	0.14
2001	1931	4740	0.02	0.80	0.04	0.10
2002	1773	4226	0.20	0.32	0.26	0.19
Average length in Port Moller catch (mm)			509.00	522.00	564.00	572.00

(*b*) Returns of each age class to Bristol Bay and June temperature anomalies in Cold Bay, Alaska.

	Total returns to fishery					
Year	Age 1.2	Age 2.2	Age 1.3	Age 2.3	Total	Temperature anomaly
1987	13.5	3.2	7.0	3.5	27.2	–2.05
1988	4.9	5.1	9.7	3.0	22.7	–0.53
1989	4.7	27.3	7.0	4.0	43.0	–0.57
1990	7.0	19.7	9.9	9.5	46.1	0.40
1991	7.9	8.6	19.5	4.8	40.8	–1.00
1992	5.8	15.3	12.1	10.0	43.2	1.47
1993	6.7	17.2	9.6	17.1	50.6	0.68
1994	4.3	28.3	7.2	8.9	48.7	–0.90
1995	9.8	34.2	7.2	8.8	60.0	–0.22
1996	3.9	4.7	18.7	8.7	36.0	–1.05
1997	3.8	6.3	4.8	3.4	18.3	1.58
1998	6.2	2.3	5.3	4.1	17.9	0.93
1999	20.1	9.6	6.7	2.7	39.1	–1.67
2000	4.1	2.6	12.5	4.0	23.3	0.32
2001	0.8	0.7	17.9	2.1	21.5	0.62
2002	4.9	6.7	3.3	2.2	17.0	1.98

Note: Because we only consider the four major age classes, proportions do not sum to one. "Temperature anomaly" refers to the June air temperature anomaly in Cold Bay, Alaska (°C).

fish crossing station x (given that the run is normally distributed in space with the parameters μ_{dy}, σ_{dy}), multiplied by the scaling factor S_{dy}". The model is fit to the data by minimizing the square of the difference between the observed cumulative station index and that predicted by eq. 6 for each station sampled:

$$(7) \qquad SSQ_{dy} = \sum_{x} (C_{xdy} - \hat{C}_{xdy})^2$$

where all observations are treated as independent. The area of this estimated normal distribution is the cumulative integral index. Because the area under any normal density function is equal to one, the integral of the function is equal to the scaling factor (S_{dy}):

$$(8) \qquad C_{I_{dy}} = S_{dy} = S_{dy} \int_{-\infty}^{\infty} \frac{1}{\sigma_{dy}\sqrt{2\pi}} \exp^{-\left(\frac{(x-\mu_{dy})^2}{2\sigma_{dy}^2}\right)} dx$$

The age-specific index is calculated by multiplying the total index by the proportion of the total sampled fish through day d which were of a given age class.

$$(9) \qquad C_{I_{ady}} = p_{ady} C_{I_{dy}}$$

Forecasts from indices

The following analysis can also be performed for any day of the test fishing season (for notation and terms see Appendix A).

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Fig. 4. Historical cumulative station indices and corresponding estimated integral indices. Solid bars represent 30 June cumulative station indices from the traditional sampling stations 2, 4, 6, and 8. Hatched bars represent those from additional stations fished regularly in recent years. Curves represent the best-fit normal distributions to the CPUE (catch-per-unit-effort) data with the parameters $\mu_{June30,y}$, $\sigma_{June30,y}$, and $S_{June30,y}$. All y axes are scaled to 1200 index points.

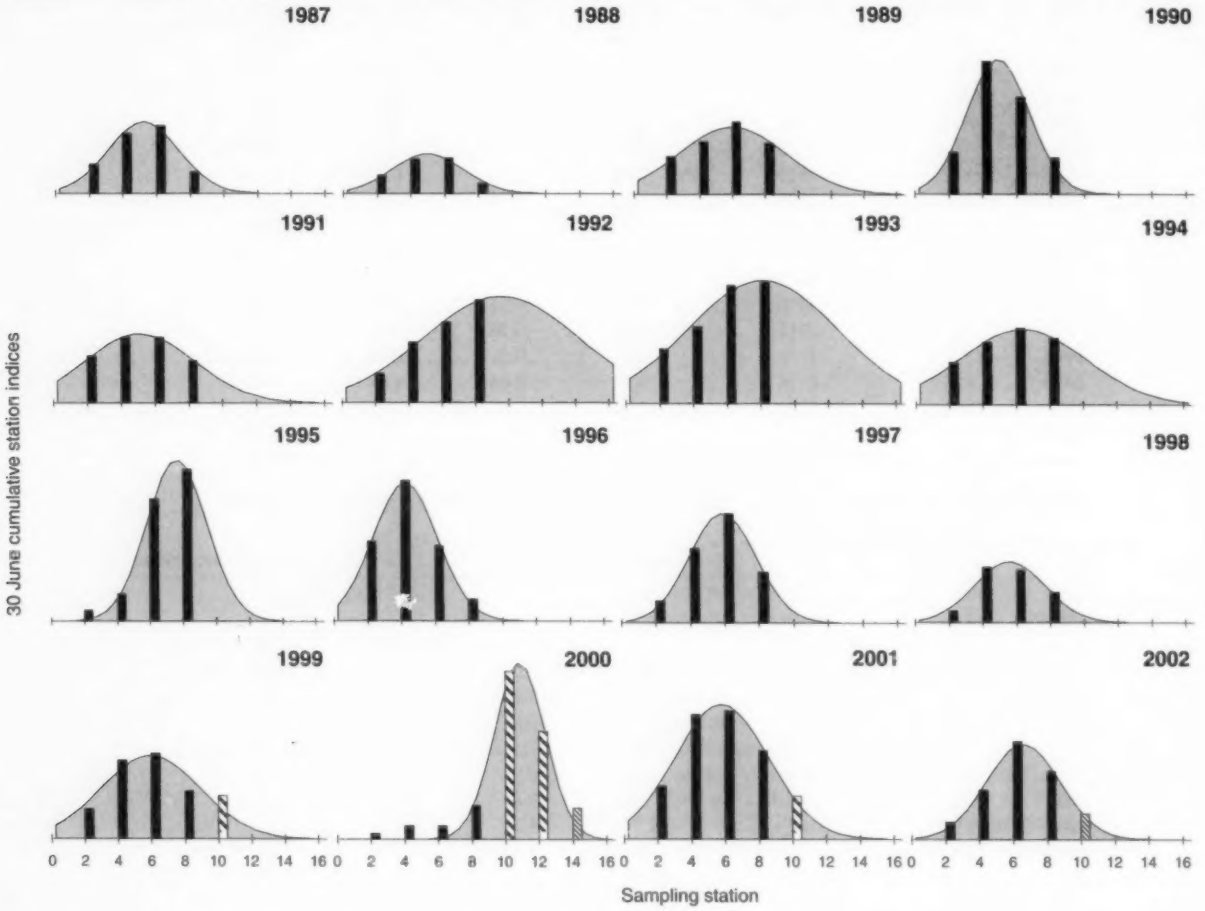
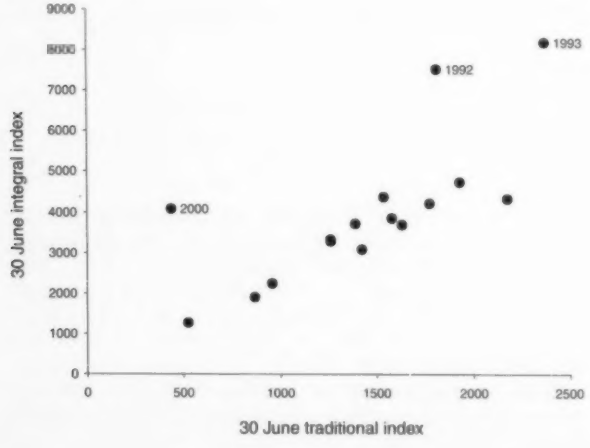


Fig. 5. Integral indices plotted against corresponding traditional indices.



The traditional prediction model contains two parameters, a slope and an intercept (eq. 4; Helton 1991). The slope can be interpreted biologically as the proportion of the incoming run that we expect to sample beyond a given run size. The intercept can be interpreted as the largest run size at which we will sample no fish. Because neither migration patterns nor vulnerability to the test fishing gear have been demonstrated to change with run magnitude, the model is far from intuitive. We propose instead a model with only multiplicative effects, where we expect to sample some proportion of the incoming run (of age class a), regardless of run magnitude. Essentially, the intercept term is dropped, and eq. 10 can be stated as "the run size prediction for age group a on day d is equal to the cumulative age-specific index on that day multiplied by the average historical return of that age class per index point on that date":

$$(10) \qquad \hat{R}_{ady} = q_{ad} C_{ady}$$

where q_{ad} is the average historical return of age a per index point on day d. The total run size prediction is calculated by summing age-specific predictions:

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Fig. 6. Return of (*a*) age 1.2, (*b*) age 2.2, (*c*) age 1.3, and (*d*) age 2.3 (all in millions of fish) plotted against the respective 30 June age-specific cumulative integral indices.

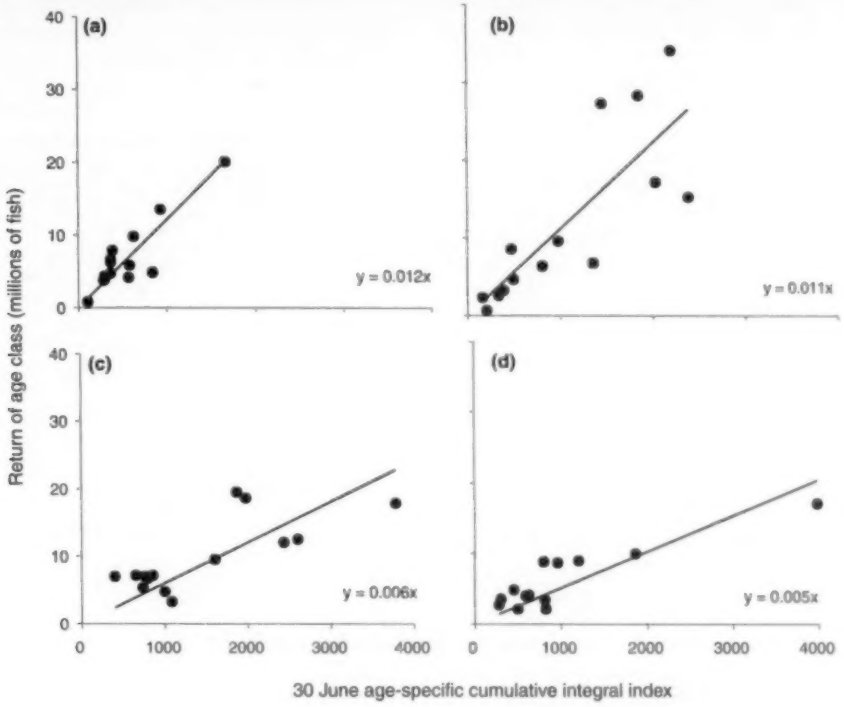
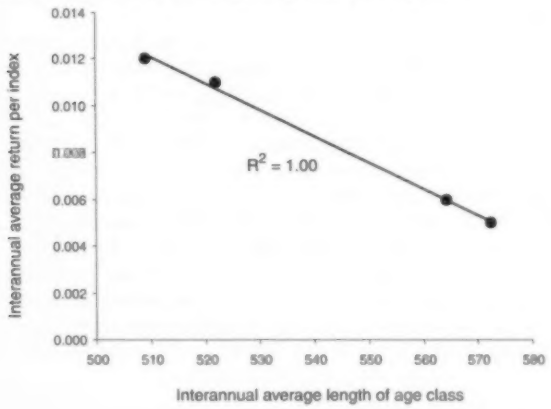


Fig. 7. Interannual average returns per index point plotted against the interannual average length of each age class.



$$(11) \quad \hat{R}_{dy} = \sum_{a} \hat{R}_{ady}$$

At an additional level of model complexity, the age-specific run size prediction R_{ay} can also be multiplied by a "temperature factor", which is equal to the exponent of the deviation from average temperature ($T_{dy} - \overline{T}_d$) multiplied by an age-specific temperature parameter (g_{ad}):

$$(12) \quad \hat{R}_{ady} = q_{ad} C_{ady} (\exp(g_{ad}(T_{dy} - \overline{T}_d))$$

In this case, the total run size forecast is also calculated using eq. 11.

We carried out our analysis using data from 30 June of each year, approximately two-thirds of the way through the test fishing season. This date was chosen because it is halfway through the traditional forecasting period (20 June – 10 July) and is still relatively early in the commercial fishing season. During the period for which catches and escapements have been recorded by ADF&G (1956–2002), an average of 16% of the run has returned by this date (L. Fair, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518, personal communication). We increased the number of parameters in the model sequentially by including first one catchability parameter (q) for all fish, then including one q for each ocean age, and finally including one q for each age. We considered temperature parameters in the same combinations. The appropriate model complexity was determined by comparing predictive fits for the past 5 years. We initially applied the same combinations of parameters to the traditional index (eq. 2), but performance of the integral index was superior, and for the sake of brevity, we show results only for the latter. We provide a summary of the data used in the exercise (Table 2).

Results

Integral indices were calculated from cumulative station indices (Fig. 4), and integral indices were plotted against corresponding traditional indices (Fig. 5). Although the linear relationship between the integral and traditional index is evident, the integral index deviates from the basic relationship in years in which the fish were distributed further offshore (1992, 1993, 2000). Visual comparison of these years,

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Fig. 8. Ratio of the actual to predicted return of (*a*) age 1.2, (*b*) age 2.2, (*c*) age 1.3, and (*d*) age 2.3 (all using the age-specific integral indices multiplied by age-specific return per index parameters) plotted against the year's June Cold Bay air temperature anomaly. The 2.3 age class (*d*) is illustrated both with (solid line) and without (○, broken line) the outlying point.

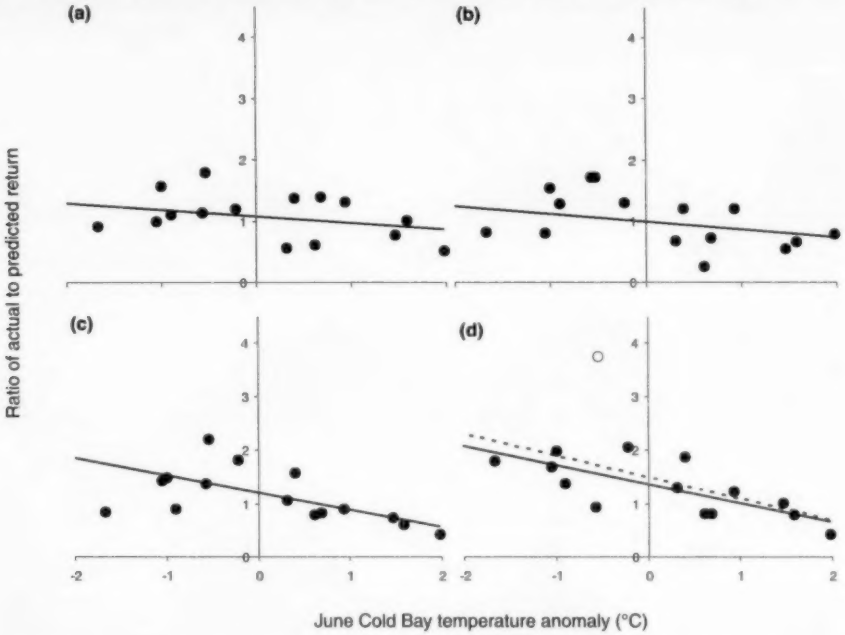

Table 3. Regression statistics for the ratio of expected to observed returns as a function of the Cold Bay temperature anomaly (*a*) before the outlier in the 2.3 age class is omitted and (*b*) after the omission.

Age	Slope	Intercept	R^2	*p*	*n*
(*a*) Before outlier omitted.					
1.2	–0.11	1.08	0.12	0.182	16
2.2	–0.13	1.00	0.12	0.191	16
1.3	**–0.33**	**1.22**	**0.44**	**0.005**	**16**
2.3	**–0.40**	**1.50**	**0.36**	**0.014**	**16**
(*b*) After outlier omitted.					
1.2	–0.11	1.08	0.12	0.182	16
2.2	–0.13	1.00	0.12	0.191	16
1.3	**–0.33**	**1.22**	**0.44**	**0.005**	**16**
2.3	**–0.35**	**1.37**	**0.60**	**0.001**	**15**

Note: Bold type indicates significance at the $\alpha = 0.05$ level.

particularly for the year 2000, illustrates the inadequacy of the traditional index (Fig. 4).

We found a greater than twofold range of variability in historical return-per-age-specific index point. Historical average RPI values (trendline slopes) ranged from 0.012 for age 1.2 fish to 0.005 for age 2.3 fish (Fig. 6). When those average RPI values were plotted against the interannual average fish length of each age class, a linear decrease in RPI with increasing fish size is clearly indicated (Fig. 7).

The ratio of actual to predicted return (where return is predicted using only the age-specific integral index) is used as an index of how greatly the CPUE was inflated or deflated each season. These ratios are correlated with deviations from average temperatures (Fig. 8). Although regressions between this ratio and the temperature anomaly were not consistently significant (Table 3*a*), a strong trend in both the fitted slope and the coefficient of determination (R^2) can be observed (Fig. 9).

The obvious outlier in the case of the 2.3 age class is likely due to the very small expected and observed return of the age class in that year ($\hat{R}_{2.3\text{June}30,1998} = 0.8$, $R_{2.3,1988} = 3.0$, in millions of fish, where all data from 1987–2002 are considered), and the absolute error, 2.2 million fish, is relatively small in absolute terms. The Bonferroni test for outlying cases (Neter et al. 1996) results in the point being discarded ($p < 0.001$), after which the relationships, particularly that with the R^2 value, are much stronger (Table 3*b*; Fig. 9).

As can be predicted (i.e., from Figs. 6–9), the best predictive model used the integral index, catchability parameters for each ocean age group, and a temperature parameter for 3-ocean group (Table 4; Fig. 10).

$$\hat{R}_{\text{June30, y}} = 0.011\sum(C_{I_{1.2,\text{June30, y}}}, C_{I_{2.2,\text{June30, y}}}) + 0.006\left(\sum(C_{I_{1.3,\text{June30, y}}}, C_{I_{2.3,\text{June30, y}}})\right) \times \left(\exp\left(-0.34\left(T_{\text{June30, y}} - \overline{T}_{\text{June30}}\right)\right)\right) \quad (13)$$

The retrospective and predictive fits of the data to the chosen model are a substantial improvement over those of the traditional forecasting model. The model has an average retrospective error of 6.7 million fish or 21% (compared with 8.7 or 33% with the traditional model). It has an average predictive error for the last 5 years of 6.4 million fish, or 32%, compared with 12.5 million or 65% with the traditional model (Table 4; Fig. 10).

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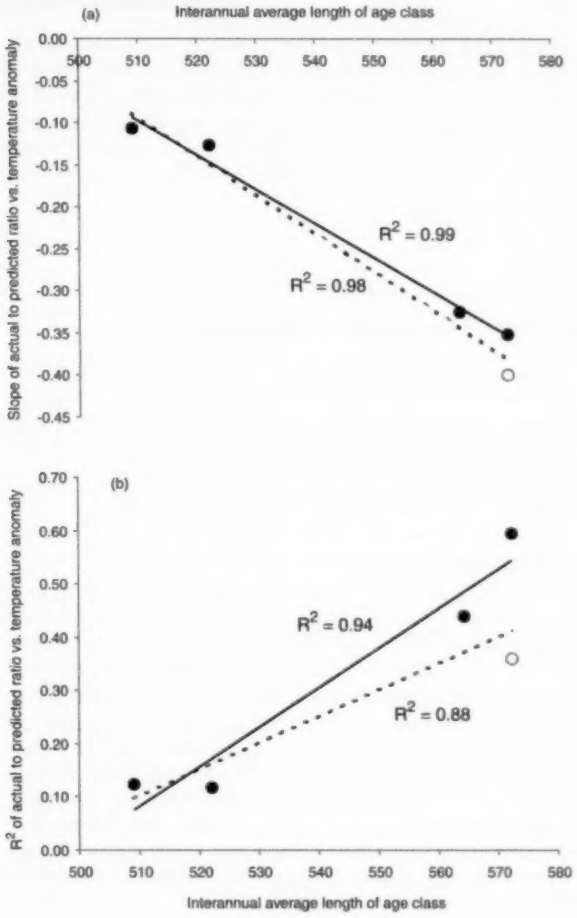
Fig. 9. (*a*) The slope of the actual to predicted return plotted against the temperature anomaly as a function of the interannual average size of each age class, and (*b*) the coefficient of determination (R^2) of those relationships plotted against the interannual average sizes. Included is the relationship before the outlier in the 2.3 age class has been excluded (○, broken line) and after it has been excluded (solid line).



Discussion

Migration

Several studies have established significant differences in migratory timing between jacks and non-jacks (Jonsson et al. 1990; Hansen and Jonsson 1991), but we are unaware of any study establishing differences between the return timing of other age classes. If we assume that the CPUE variation in accordance with environmental temperatures is at least partially due to a shift in migration timing, then the relationship between fish size and the magnitude of the "temperature effect" is notable with respect to proposed mechanistic explanations. With regard to migration timing, two basic hypotheses (which are not mutually exclusive) have been set forth: the traditional hypothesis is that of variable maturation (Karlsson et al. 1994) and (or) migration rates (Burgner 1980; Hodgson 2000). French and Bakkala (1974) reported that during the winter at sea Bristol sockeye separate into immature and maturing groups. Those that will mature migrate towards to Bristol Bay in the spring, with the major proportion entering the Bering Sea through passes in the Aleutian Island chain. Burgner (1980) found that the average of May and June air temperatures on the Alaskan Peninsula predicted Bristol Bay return timing more accurately than earlier months and attributed the relationship to "oceanographic conditions the fish encounter in their final migration south of the Aleutians through the passes, and northeastward in the Bering Sea". Hodgson's (2000) work on Bristol Bay's migratory timing found June SSTs to provide stronger correlations than either April or May, lending further support to the hypothesis that migration rates are the primary causal mechanism for shifts in return timing.

A more recent hypothesis, put forward by Blackbourn (1987), is that salmonid return timing is dependent primarily on the variable starting point from which the homeward migration is commenced. Sockeye are believed to seek out areas with SSTs from 4 to 8 °C during the winter, presumably to optimize metabolic rates during poor feeding conditions (Ishida et al. 2000; Nagasawa 2000). Blackbourn (1987) proposed that differences in timing are caused by differences in ocean distribution resulting from differences in the latitude of this temperature range at the time that spawning migration begins. Blackbourn (1987) found that increased SSTs were correlated with earlier returns of Alaskan and Skeena River stocks and later returns of Fraser River and Washington stocks, lending support to the hypothesized causal mechanism. The Blackbourn (1987) study did not include Bristol Bay stocks.

It is not difficult to interpret the observed results within the context of the traditional migration rate hypothesis. Larger fish are capable of greater swimming speeds and would therefore be expected to possess the ability to adjust swimming speeds more dramatically in accordance with environmental cues. However, if the ocean distribution hypothesis is accepted, the results are more problematic. If the timing of the 3-ocean component is shifted substantially in years of extreme temperatures but that in the 2-ocean component is shifted less, implications within the context of Blackbourn's (1987) hypothesis are that the ocean distribution of the 3-ocean component is shifted more dramatically than that of the 2-ocean component.

It is important to note that the relationship between temperature and CPUE inflation may not be due solely or even largely to altered migration timing. For example, results may be partially due to differences in swimming depth, particularly for larger, older fish. Westerberg et al. (1999) found that migrating Atlantic salmon (*Salmo salar*) in the Baltic Sea completed their homeward migration at a significantly shallower depth during the anomalously warm summer of 1997 than in 1996. Although we conceptualize the temperature factor as a timing factor, there are alternative explanations that may account for at least part of the variation.

Calculation of accurate run timing indices for the Bristol Bay sockeye return is problematic because of variable time lags between commercial catches and escapements. Burgner's (1980) publication does not specify whether or not this issue was accounted for in calculating the date on which 50% of

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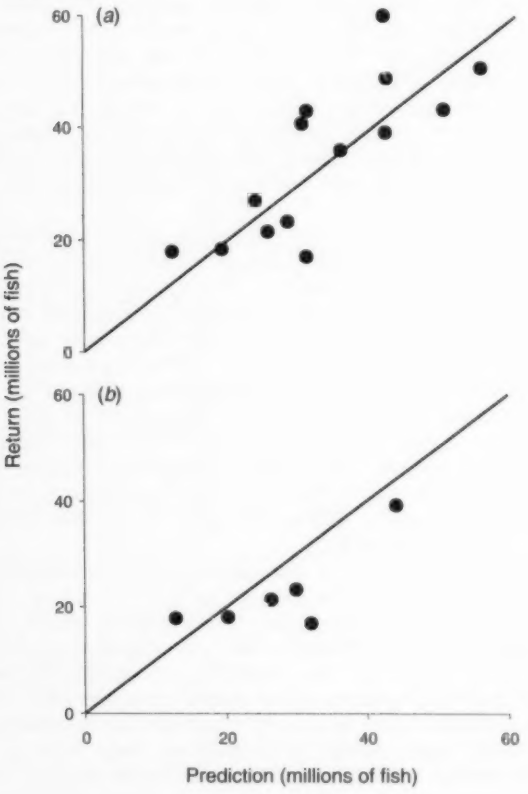
Table 4. Retrospective and predictive fits of data to model selected.

	Retrospective fits				Predictive fits		
Year	Return	Prediction	Error	% Error	Prediction	Error	% Error
1987	27.2	23.8	–3.4	–13			
1989	43.0	31.0	–12.0	–28			
1991	40.8	30.3	–10.5	–26			
1992	43.2	49.8	6.6	15			
1993	50.6	55.1	4.5	9			
1994	48.7	42.0	–6.7	–14			
1995	60.0	41.7	–18.3	–31			
1996	36.0	35.7	–0.3	–1			
1997	18.3	19.0	0.7	4	20.2	1.9	10
1998	17.9	12.1	–5.8	–32	12.8	–5.1	–28
1999	39.1	41.9	2.7	7	44.2	5.1	13
2000	23.3	28.2	4.9	21	29.8	6.5	28
2001	21.5	25.5	4.1	19	26.5	5.0	23
2002	17.0	30.7	13.7	81	32.0	15.0	88
Absolute average			6.7	21		6.4	32

Fig. 10. (*a*) Retrospective and (*b*) predictive fits of the data to the chosen model.



the run had returned. Hodgson's (2000) study used lag times estimated visually from plots of commercial catches and escapements by day for each major river, where valleys in the catch plots are matched with peaks in the escapement plots. To our knowledge, no attempt has been made to quantify the timing returns of individual age classes. We feel that if an accurate model of migration into and between commercial harvest areas and counting towers were developed, a comparison between the timing of age-specific returns and environmental temperatures would be useful with respect to proposed mechanisms governing migration timing.

In-season forecasting

With this exercise, we have illustrated several ways in which to adjust run size or escapement estimations that can be applied to almost any test fishery. Most Pacific salmon species (*Onchorhynchus* spp.) display considerable variability in the age composition of returns, and most test fisheries collect scale samples that can be aged as soon as they are transported to a scale-reading facility. Data on environmental conditions are also readily available in many cases and can often be collected during the test fishing process (i.e., water temperatures, water flows). In summary, test fishery data sets analyzed for factors influencing catchability may become much more useful as in-season abundance estimators with little or no increase in cost.

The advantage of the integral index in years with anomalously offshore centers of distribution illustrates the advantage of flexible sampling methods. A sampling program aimed at estimating the area under a curve rather than a simple sum of indices can allow for flexibility in sampling regimes, enabling managers to adjust immediately to shifts in spatial distribution. Moreover, because the integral can be estimated for all years of test fishery operation, a spatial shift in effort allocation does not entail discarding data collected in early years.

Although this analysis provides a means to adjust CPUE data for factors significantly affecting catchability on a seasonal scale, further improvement may be possible by examining the data on a set-by-set basis. In the case of the Port Moller test fishery, records are kept for each set made by the sampling vessel, including the time of day, tidal activity, weather conditions (temperature, wind, wave action, cloud cover), and the total number of fish caught. If historical data

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were examined on the level of individual sets, it would be possible to address issues that cannot be addressed with data on the daily or seasonal level, such as tidal influences and the effects of gear saturation. A detailed analysis of these set-specific data may further increase forecasting accuracy.

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Appendix A

x a given station location along the sampling transect in units of numbering along the transect (2, 4, 6, 8, 10, 12, and 14 have been used thus far; Fig. 1)

I_{xiy} the catch-per-unit-effort (CPUE) index at station x on day i of year y

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$\hat{C}_{xdy}$ the predicted cumulative station CPUE index at station x on day d of year y

C_{xdy} the actual cumulative station CPUE index at station x on day d of year y

μ_{dy} the estimated mean location of the density of fish across the transect on day d of year y in units of transect location (Fig. 1)

σ_{dy} the estimated standard deviation about the mean location of fish density on day d of year y in units of transect location (Fig. 1)

S_{dy} a year-specific scaling factor relating the probability density function to actual CPUE on day d of year y

$C_{I_{dy}}$ the estimated cumulative integral index on day d of year y

p_{ady} the proportion of the cumulative test-fishery catches which was of age class a on day d of year y

$C_{I_{ady}}$ the estimated age-specific cumulative integral index of age a on day d of year y

T_{dy} the average of daily high and low air temperatures in Cold Bay, Alaska, between June 1st of year y and day d of year y

$\overline{T}_d$ the historical average of daily high and low air temperatures in Cold Bay, Alaska, between June 1st and day d. (Average is calculated from the years 1987–2002, all of the years that were used in the analysis.)

q_{ad} the model parameter for returns-per-index point of age a on day d

g_{ad} the model parameter for the temperature the factor for the returns-per-index point of age a on day d

$\hat{R}_{ady}$ the predicted return (in millions of fish) of age a on day d of year y

R_{ady} the actual return (in millions of fish) of age a on day d of year y

$\hat{R}_{dy}$ the predicted return (in millions of fish) on day d of year y

R_{dy} the actual return (in millions of fish) on day d of year y

Retrospective error the average absolute prediction error when the entire data set is fit to the model

Predictive error the average absolute prediction error for the last five years (1997–2002) when only the data available before each year are used to predict that year's return

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Within-basin fish assemblage structure: the relative influence of habitat versus stream spatial position on local species richness

G. Grenouillet, D. Pont, and C. Hérissé

Abstract: Local species richness (LSR) in stream fish assemblages is related to both local habitat conditions and stream spatial position. In this study, we examined the within-basin distribution of LSR in the Upper Saône River (France). We describe the longitudinal patterns in LSR and assess the relative effects of both local habitat and spatial (upstream and downstream) influences on species richness. We showed that among the different local habitat variables, only stream width and gradient significantly influenced LSR. Spatial factors also influenced the within-basin distribution of LSR and resulted in spatial autocorrelation, highlighting contagious biotic processes in structuring stream fish assemblages. However, we did not confirm other published predictions that headwater streams entering large rivers directly should have greater species richness. The spatial autocorrelation was only significant downstream (from 4th- to 7th-order streams), suggesting that the relative importance of local habitat and biotic processes may depend on the position along the longitudinal gradient.

Résumé : Dans les systèmes lotiques, la richesse spécifique locale (LSR) des assemblages piscicoles dépend à la fois de conditions locales d'habitat et du positionnement spatial du cours d'eau. Dans cette étude, nous avons étudié la distribution de LSR dans le bassin de la Haute-Saône (France). Nous avons abordé les effets relatifs de facteurs locaux d'habitat et de facteurs spatiaux (amont et aval) sur la richesse spécifique. Parmi les variables locales d'habitat, seules la largeur et la pente du cours d'eau influencent significativement LSR. Des facteurs spatiaux interviennent également dans la distribution de LSR et induisent une autocorrélation spatiale, révélant ainsi des processus biotiques contagieux qui structurent les communautés piscicoles. Cependant, nous n'avons pas pu vérifier les prédictions selon lesquelles des cours d'eaux de tête de bassin se jettant directement dans de grands cours d'eaux devraient avoir des richesses spécifiques plus élevées. L'autocorrélation spatiale ne concernait que les cours d'eau aval (ordre 4 à 7), suggérant ainsi que l'importance relative de l'habitat local et des processus biotiques pourrait dépendre de la position le long du gradient longitudinal.

Introduction

Most natural ecological phenomena display geographical patchiness (e.g., Legendre 1993), and a central idea in community ecology is that the spatial heterogeneity in community structure is the result of the combined effects of environmental and biotic processes. These spatial patterns (i.e., spatial autocorrelation) come either from environmental influences or from community processes. Studies on the spatial structuring of communities have clearly underlined the importance of integrating space in the study of structure in species distribution (Borcard et al. 1992; Legendre 1993; Cooper et al. 1997). However, very few studies dealing with spatially distributed data have taken the spatial structure of their observations into account. Consequently, the relative importance of physical vs. biotic regulation of locally occurring species remains poorly investigated.

In lotic systems, space can be described as a complex hierarchical network of individual reaches. From the perspective of fishes, both of the views of streams as large continua or as patchy mosaics seem important (Matthews 1998). Taking the drainage into account, the drainage structure is thus critical to understanding fish distribution. In this context, two spatial features have been shown to influence stream fish assemblages: (*i*) the position along the upstream–downstream gradient, and (*ii*) the spatial position of the stream within the drainage network.

The upstream–downstream gradient is probably the most well-known, large-scale pattern in stream fish assemblages. Longitudinal changes along physical and chemical gradients generally reflect an increase in fish species richness with increasing stream size (reviewed in Matthews 1986). This typical longitudinal pattern has been well discussed, with different explanations being advanced such as habitat diversity (Gorman and Karr 1978), differential rates of immigration and extinction (Power et al. 1988), or sampling phenomenon (Angermeier and Schlosser 1989). Much of the debate on the mechanisms responsible for such a pattern has focused on the concepts of "addition" versus "replacement"

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of species from headwaters to lower mainstreams (see Matthews 1998). Whereas some authors reported an asymptote or a decrease in fish species richness in the lower part of some rivers (e.g., Oberdorff et al. 1993), most available studies have provided evidence in support of addition as a prevailing pattern, at least in rivers lacking geographical discontinuities (e.g., Welcomme 1985).

What is the influence of stream spatial position in a drainage network on the structure of fish assemblages is a poorly addressed question. This question was raised by Fausch et al. (1984), who observed higher species richness in collections near mouths of tributaries entering large rivers. Gorman (1986) first considered the effects of discontinuity on tributary streams for river fish assemblages and suggested that small streams directly joining large rivers should have different assemblages than small streams that increase gradually in size downstream. Osborne and Wiley (1992) first devoted a paper entirely to this question and examined the relationships between fish species richness and four measures of stream size (drainage area, stream order, and two measures of linkage of stream reaches). They revealed that the link magnitude of the stream below the next downstream confluence explained most of the variance in local species richness. Thus they verified the hypothesis that for streams of similar size's order, fish assemblages should have greater species richness in tributaries to the main channel than in streams located in the headwaters of a basin. This hypothesis is based on displacement of individuals within the drainage network and suggests that large river species can potentially migrate into the lower parts of tributaries. Larger streams could thus serve as a colonizing source and may provide a pool of immigrants for subsequent recolonization following a disturbance. The immigration–extinction hypothesis (MacArthur and Wilson 1967) therefore appears to be an important mechanism influencing fish assemblage structure at the drainage network scale.

To date, the study of Osborne and Wiley (1992) remains one of the key papers highlighting the influence of stream spatial position on fish assemblage structure. Although Osborne and Wiley (1992) emphasized the necessity of considering stream spatial position to better predict local fish assemblages, the theoretical and applied implications of such an approach have received little attention. More curiously, local habitat conditions and stream spatial position have rarely been examined together. Consequently, addressing the question of the relative influence of local habitat and stream spatial position on local species richness remains of crucial interest and should be helpful in the debate on the relative importance of physical vs. biotic regulation of stream fish assemblages.

This study investigates river fish assemblages in the Upper Saône River (France) in relation to both local habitat conditions and stream spatial position. Our data set covered a wide range of stream habitats in which both fish assemblages and local habitat conditions were described. We examined local species richness with the objectives of (*i*) describing the within-basin distribution of local fish species richness, (*ii*) examining the effects of local habitat on species richness, (*iii*) assessing the evidence for upstream and downstream influences on local species richness, and (*iv*) determining the relative importance of both habitat and spatial factors.

Materials and methods

Site selection

As part of the "Fisheries Orientation Schemes" (Souchon and Trocherie 1990), the French river network has been subjected to systematic investigations using a standardized method since 1982. Depending on their geomorphologic, physical, and chemical characteristics, rivers have been divided into ecologically homogeneous sections in which both habitats and fish assemblages have been described (Changeux and Pont 1995).

The study area (Upper Saône River in northeastern France) covers approximately 19 600 km^2 and consists of two major subbasins: the Saône River (12 300 km^2) and the Doubs River (7300 km^2). The whole river network contains 113 streams with a total length of about 3028 km (2115 km and 913 km for the Saône River and the Doubs River, respectively). Within these 113 streams, the investigation method defined 295 adjacent sections, hereafter called sample sites (Fig. 1). These sites encompassed a wide range of stream habitats: stream order (sensu Strahler 1957) varied between 1 and 7, and stream altitude ranged from about 930 m (the sources of the Doubs River) to 173 m at the confluence between the Doubs and Saône rivers. Despite some hydraulic modifications, the sample sites were characterized by the absence of impassable barriers (e.g., dams) to fish. Therefore, fish have had the opportunity to colonize all of the tributary streams in the basin, and from a biogeographical viewpoint, this river network was thus of primary interest.

Fish and habitat sampling

At each site, fish distribution data were collected by the Conseil Supérieur de la Pêche. Standardized electrofishing methods were used during low flow periods (from August to October), and depending on river width and depth, two different sampling methods were used. When it was possible (small rivers), each site was sampled by wading. In large rivers, sampling was undertaken by boat in nearshore areas (see Oberdorff et al. (2001) for more details). Fish assemblages were described in presence and absence terms. Lists of fish species were compiled from this database, and the number of fish species occurring in a site defined the local species richness (LSR). Most of the sites were sampled once. For sites sampled many times, observations were pooled so that interannual variability could not be addressed in this study.

At each site, geomorphologic, chemical, and climatic variables were used to describe local environmental conditions. The geomorphologic variables used were gradient (GRA, ‰) and stream width (WID, m). Water quality (QUA) was coded semiquantitatively from 1 (absence of pollution) to 5 (highly polluted) as defined by the Water Quality Index developed by the French Water Agency. Climatic variables were not available for each site. To describe local climatic conditions, data were thus interpolated according to the geographical coordinates of upstream and downstream positions

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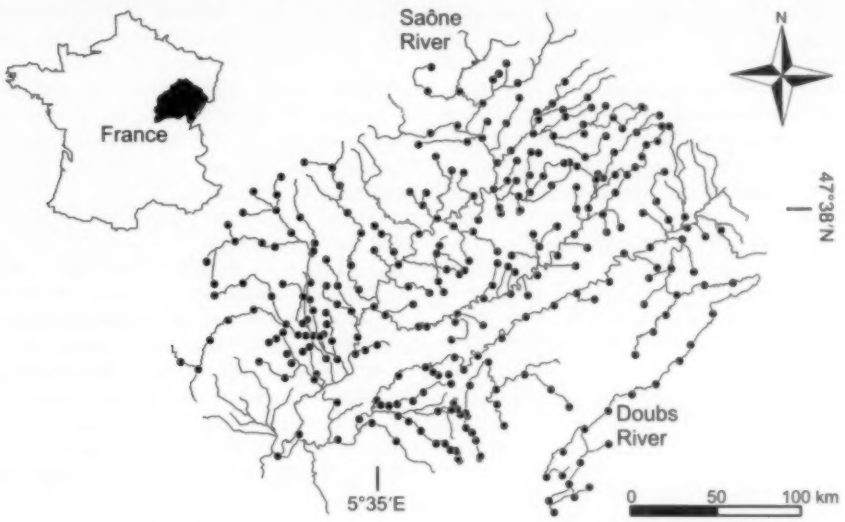
Fig. 1. Map of the Upper Saône River drainage in northeastern France. Solid circles (●) indicate the upstream locations of the 295 sample sites.



derived from IGN (Institut Géographic National) topographic maps (1:25 000 scale) and using mean monthly values supplied by the French Meteorological Office. Therefore, two climatic variables were generated for each site: July mean air temperature (T_{July}) and January mean air temperature ($T_{January}$). We then defined two climatic variables related to temperature requirements of fish species: mean annual temperature (T_{mean}) and annual thermal amplitude (T_{amp}):

$$T_{mean} = (T_{July} + T_{January})/2$$

$$T_{amp} = (T_{July} - T_{January})/2$$

These two variables, which are potential explanations for fish spatial distribution patterns (Oberdorff et al. 2001), are therefore potential correlates of local fish species richness.

Stream spatial position

Among the geomorphic variables traditionally used to describe lotic systems, drainage area, stream order (Strahler 1957), and link magnitude (Scheidegger 1965) reflect stream size and describe upstream characteristics relative to the entire subcatchment upstream of a given site (Osborne and Wiley 1992). Although stream order incrementally increases only below the confluence of two streams of the same order, link magnitude accounts for the addition of tributaries of order $x - n$ ($n \geq 1$) to a section of order x. As a result, the junction of two streams of unequal order does not affect stream order, whereas link magnitude increases below each confluence and finally represents the number of 1st-order segments upstream of a given site (see Osborne and Wiley (1992) for more details). Catchment area (AREA) was extracted with the geographic information system (GIS) program ArcView 3.2.2 from thematic maps produced by Rogers et al. (2001). Stream order (ORDER) and link magnitude (LINK) were derived from IGN topographic maps (1:25 000 scale).

According to Osborne and Wiley (1992), we defined downstream characteristics for each site using geomorphic metrics of the next downstream site. For each site, we defined the stream order and the link magnitude of the next downstream site (downstream order (D-ORDER) and downstream link (D-LINK), respectively). These two variables were used as indices of the spatial location of a stream within the drainage network. Because biological processes (e.g., colonization dynamics) have been proposed to explain downstream influences, we used local species richness of the next downstream site (downstream LSR (D-LSR)) as a downstream characteristic potentially influencing local fish assemblages.

Data analysis

Within-basin distribution of local species richness

We described within-basin distribution of LSR by examining (*i*) spatial covariance (i.e., autocorrelation) in LSR and (*ii*) the relationship between LSR and stream order. According to Cliff and Ord (1973), spatial covariance for the vector $\boldsymbol{X}$ is defined by the product

$$\boldsymbol{X}^t \frac{1}{2m} \boldsymbol{M}\boldsymbol{X}$$

where $\boldsymbol{X}^t$ is the transpose of $\boldsymbol{X}$, m is the total number of pairs of neighbors, and $\boldsymbol{M}$ is the neighborhood matrix, so that only neighbor pairs of sites are used to calculate the spatial covariance of $\boldsymbol{X}$. We used randomization tests for spatial autocorrelation in LSR. In comparison with more standard statistical methods, the main advantage of these tests is that it is relatively easy to take into account the peculiarities of the situation of interest and no particular assumption is made on the distribution of the test statistic (Manly 1994). We took into account the spatial structure of the river network by means of a neighboring relationship in which only successive sample sites along the river network were neighbors. Monte Carlo permutations were used to test if the observed covariance in neighbor LSR values differed from those ex-

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pected under the null hypothesis (i.e., LSR is randomly distributed within the river network). To do this, we permutated the LSR observed among the sampling sites and calculated the resulting covariance between neighbors. We evaluated the significance of the observed covariance by comparing it with the distribution of 1000 random permutation values obtained under the null hypothesis (Manly 1994). If less than 5% of the permutation values were higher than the observed one, we concluded that LSR was not randomly distributed but correlated with the neighborhood. Spatial autocorrelation tests were performed using (*i*) the whole data set (295 sampling sites) and (*ii*) separate subsets for each stream order.

Local habitat determinants of LSR

We tested the hypothesis that fish assemblages were regulated by local habitat conditions by using the multiple linear regression model (model 1):

$$(1) \quad \mathrm{LSR} = a + b(\mathrm{GRA}) + c(\mathrm{WID}) + d(\mathrm{QUA}) + e(T_{\mathrm{mean}}) + f(T_{\mathrm{amp}}) + \varepsilon$$

Before the analyses, a log transformation was applied to GRA, WID, T_{mean}, and T_{amp} to minimize effects of extreme values. After transformation, only GRA was normally distributed (Lilliefors test; $P = 0.330$), but all variables showed bell-shaped, unimodal distribution and low colinearity.

We used stepwise forward regression (Sokal and Rohlf 1995) to identify significant variables, which explained most of the variance in LSR. At each step, a new variable was added to the model if it significantly ($P < 0.05$) reduced the unexplained variance using the Akaike criterion.

Upstream and downstream influences on LSR

We tested the hypothesis that stream spatial location influenced fish assemblages by comparing the least-squares fits for spatial location characteristics and fish assemblage descriptors. Variables compared included upstream (ORDER, LINK, and AREA) and downstream (D-ORDER, D-LINK, and D-LSR) characteristics. Following Osborne and Wiley (1992), these variables were tested against LSR. Then we also tested these variables against the residuals from model 1 after having removed the effects of local habitat conditions.

Relative importance of both habitat and spatial factors

Because only D-LSR appeared to influence LSR after having removed local habitat effects, we used D-LSR as a spatial descriptor potentially influencing LSR. Total LSR variation was partitioned into four independent components: (*i*) a local habitat effect; (*ii*) a D-LSR effect; (*iii*) a combined effect extracted by both habitat factors and D-LSR; and (*iv*) a residual (see Whittaker 1984). Finally, we examined whether the influence of D-LSR on LSR differed between stream orders.

Results

Environmental characteristics

Local habitat conditions and stream spatial position were described at the 295 sampling points (Table 1). For local habitat variables, the two surrogates of stream size (GRA and WID) ranged from 0.1‰ to 126.0‰ and from 0.8 m to 175.0 m, respectively. T_{mean} and T_{amp} ranged from 8.0 °C to 10.5 °C and from 16.0 °C to 18.5 °C, respectively. GRA, WID, and T_{mean} differed significantly ($P < 0.05$) between stream orders, whereas there was no significant difference for T_{amp} and QUA (Table 1).

LINK ranged from 1 to 398 and AREA ranged from 1 km^2 to 19 263 km^2 (Table 1). These two variables showed a similar exponential increase with stream order. Pairwise correlations between the five local habitat variables, when significant, were not high (Table 2). The highest correlation observed involved GRA and WID ($R^2 = 40.3\%$, $P < 0.0001$). For the five descriptors of stream spatial position, correlation ranged from $R^2 = 36.8\%$ (D-ORDER and AREA) to 91.4% (LINK and ORDER), and these variables were all significantly and positively correlated (Table 2).

Correlations between local habitat and stream spatial position descriptors showed that GRA, WID, and T_{mean} were significantly correlated with the five spatial position descriptors, with the highest correlation between WID and AREA ($R^2 = 71.9\%$, $P < 0.0001$), negative correlations between GRA and spatial descriptors, and positive correlations between T_{mean} and spatial descriptors.

Within-basin distribution of LSR

A total of 36 fish species were collected, with 35 and 36 species from the Doubs and the Saône basins, respectively. Twenty-nine species were considered as being native to the studied area (Changeux and Pont 1995). LSR did not significantly differ between the two basins (one-way analysis of variance (ANOVA) test, $P > 0.05$), and LSR ranged from 0 to 29 species (mean 9.63 ± 6.75) (Fig. 2). LSR increased along the upstream–downstream gradient, but this typical longitudinal pattern did not fit in with a linear relationship. The mean number of fish species increased from five in 1st-order streams to 25 in 7th-order sites, but although LSR regularly increased from 1st- to 5th-order sites, an abrupt increase was apparent from 5th- to 6th-order sites (Fig. 3).

According to geographical coordinates of sample sites, LSR was clearly not randomly distributed but exhibited high spatial autocorrelation at the basin scale, illustrating the well-known increase in fish species richness with increasing stream size (Fig. 2). Results from randomization tests based on the neighboring relationship between sites revealed high spatial covariance in LSR (Table 3). None of the random permutations generated covariance values higher than the observed one, so we concluded that LSR was significantly ($P < 0.001$) correlated to the neighborhood space. However, when examining spatial covariance for each stream order, permutation tests then indicated that LSR was not spatially autocorrelated among sites from 1st- to 3rd-order streams. For 4th- to 7th-order streams, observed spatial covariance in LSR was significantly higher than that obtained from random permutations (Table 3).

Local habitat determinants of LSR

Results from the multiple regression model of LSR versus local habitat variables (model 1) indicated that LSR was only influenced by two surrogates of stream size, stream width and gradient, with residuals normally distributed (Lilliefors test; $P = 0.180$). LSR was positively correlated

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Table 1. Characteristics of local habitat, spatial position, and fish variables of the Upper Saône River in northeastern France.

		Stream order							
Variables		1 (N = 55)	2 (N = 50)	3 (N = 48)	4 (N = 60)	5 (N = 39)	6 (N = 31)	7 (N = 12)	P
Local habitat	GRA	14.89a (19.85)	6.93b (11.74)	4.24b (7.26)	2.44b (1.90)	1.76b (1.70)	0.66b (0.37)	0.21b (0.15)	<0.0001
	WID	4.01a (2.75)	5.75a (5.82)	8.09a (7.01)	12.25a (6.30)	29.05b (15.06)	62.29c (36.45)	94.58d (44.01)	<0.0001
	T_{mean}	9.52a (0.69)	9.86a (0.69)	9.79a (0.75)	9.87a (0.64)	9.56a (0.87)	10.26b (0.32)	10.36b (0.21)	<0.0001
	T_{amp}	17.58a (0.39)	17.55a (0.59)	17.51a (0.54)	17.54a (0.48)	17.38a (0.45)	17.71a (0.42)	17.71a (0.43)	ns
	QUA	2.36a (1.02)	2.70a (0.92)	2.63a (0.73)	2.77a (0.97)	2.77a (1.16)	3.00a (0.80)	2.58a (0.49)	ns
Spatial position	LINK	1.00a (0.00)	2.02a (0.32)	3.73a (1.04)	7.42a (1.69)	23.36b (8.47)	60.68c (28.83)	138.50d (111.87)	<0.0001
	AREA	6.53a (29.31)	24.84a (53.15)	64.33a (78.87)	183.48a (128.87)	927.77b (512.51)	2939.03c (1994.70)	6761.17d (4669.69)	<0.0001
Fish	LSR	5.15a (3.35)	5.42a (2.42)	7.42a (3.43)	9.42b (4.22)	11.08b (5.08)	20.26c (5.61)	25.58d (2.06)	<0.0001

Note: N, number of sampling sites. For each stream order, the given characteristics are mean values with standard deviation below in parentheses. For each variable, values among stream order with a common letter are not significantly different at $P = 0.05$ (Tukey–Kramer test). Probabilities (P) (ns, not significant) are given for testing the effect of stream order on each variable (analysis of variance and χ^2 tests for continuous and categorical variables, respectively). Variables: GRA, gradient; WID, stream width; T_{mean}, mean annual temperature; T_{amp}, annual thermal amplitude; QUA, water quality; LINK, link magnitude; AREA, catchment area; LSR, local species richness.

Table 2. Matrix of pairwise correlation between environmental variables.

Variables		GRA[a]	WID[a]	T_{mean}	T_{amp}	QUA	LINK[a]	D-LINK[a]	ORDER	D-ORDER	AREA[a]
Local habitat	GRA[a]		<0.0001	<0.0001	<0.0001	0.002	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	WID[a]	–0.635		ns	ns	ns	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	T_{mean}	–0.441	0.040		<0.0001	0.012	0.024	<0.0001	0.008	<0.0001	0.033
	T_{amp}	–0.291	–0.020	0.444		0.012	ns	0.029	ns	ns	ns
	QUA	–0.239	0.108	0.212	0.211		ns	0.004	ns	<0.0001	ns
Spatial position	LINK[a]	–0.695	0.845	0.201	0.057	0.148		<0.0001	<0.0001	<0.0001	<0.0001
	D-LINK[a]	–0.638	0.603	0.309	0.198	0.227	0.726		<0.0001	<0.0001	<0.0001
	ORDER	–0.726	0.813	0.216	0.016	0.144	0.956	0.681		<0.0001	<0.0001
	D-ORDER	–0.625	0.529	0.312	0.129	0.255	0.621	0.906	0.648		<0.0001
	AREA[a]	–0.737	0.848	0.196	0.026	0.152	0.923	0.658	0.942	0.607	

Note: Variables: GRA, gradient; WID, stream width; T_{mean}, mean annual temperature; T_{amp}, annual thermal amplitude; QUA, water quality; LINK, link magnitude; D-LINK, downstream link; ORDER, stream order; D-ORDER, downstream order; AREA, catchment area. Above the diagonal, P (Bonferroni probabilities) values (ns, not significant); below the diagonal, Pearson's correlation coefficients.

[a]Variables expressed in logarithmic values.

with stream width and negatively correlated with gradient. Both variables were of similar relative importance in the model, which accounted for 63.9% of the variation in local species richness (Table 4).

Upstream and downstream influences on LSR

Among the different variables describing upstream characteristics, stream order consistently provided the best relationship with fish species richness and accounted for 53.5% of the variation in LSR (Table 5). For downstream characteristics, the best relationship was between LSR and D-LSR, whereas D-ORDER provided the weakest relationship and accounted for only 34.1% of the variation. After having removed the effects of local habitat conditions, no relationship was found between the residuals from model 1 and the geomorphologic parameters used (Table 5). Only D-LSR significantly ($P < 0.001$) influenced fish species richness, explaining 9.9% of the remaining variance in LSR.

Relative importance of both habitat and spatial factors

The five local habitat variables combined explained 65.6% of the variation in local species richness. Although D-LSR explained 40.8% of the variation in LSR, 70.3% of the variation in LSR was explained by both habitat variables and D-LSR combined. Thus, the effects of D-LSR and those of local habitat conditions were largely confounded, and the total variation in LSR could be partitioned as follows: local habitat (29.5%), local habitat + D-LSR (36.1%), D-LSR (4.7%), and undetermined (29.7%) (Fig. 4). Finally, when plotting the residuals of the local habitat model (model 1) versus D-LSR, it then appeared that (*i*) D-LSR had no significant effect on LSR in sites from low-order (≤4) streams, and

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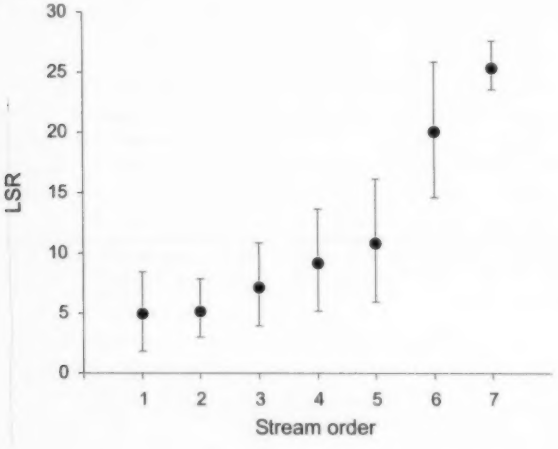
Fig. 2. Local fish species richness (LSR) within the river network. The diameters of the circles are proportional to the values represented.

Fig. 3. Local species richness (LSR; mean ± standard deviation) by stream order.



(*ii*) the relative importance of D-LSR in explaining LSR continually increased from the headwaters to large streams (Fig. 5).

Discussion

Although fish assemblages are likely to exhibit temporal (i.e., interannual) variability, we did not address temporal variability in this study because of the lack of available data for the whole data set. Here we focused on spatial fish distribution and the aim of this study was to examine the within-basin distribution of fish species richness and to test the relative importance of local habitat and spatial factors on fish assemblage structure in the Upper Saône River. The most significant way in which our study differed from most others was that the whole river network was sampled as a succession of contiguous stream segments. Moreover, the study site was characterized by the absence of large obstacles (i.e.,

Table 3. Results of Monte Carlo tests for spatial autocorrelation in local species richness.

Stream order	Spatial covariance	*P*
1 (*N* = 55)	0.212	ns
2 (*N* = 50)	0.476	ns
3 (*N* = 48)	0.134	ns
4 (*N* = 60)	4.784	0.002
5 (*N* = 39)	4.576	0.018
6 (*N* = 31)	11.931	<0.001
7 (*N* = 12)	1.450	0.005
All (*N* = 295)	17.015	<0.001

Note: Given are spatial covariance and estimated probabilities *P* (number of random permutations: 1000). *N*, number of sampling sites; ns, not significant.

Table 4. Stepwise multiple-regression model (model 1) of local species richness (LSR) vs. local habitat variables (gradient (GRA) and stream width (WID)).

Independent variables	Coefficients	*t* value	*P*	Multiple R^2
GRA[a]	−5.137 (0.556)	−9.245	<0.0001	0.639
WID[a]	6.108 (0.613)	9.970	<0.0001	

Note: Given are regression coefficients (with standard error in parentheses), *t* values, probabilities (*P*), and multiple R^2.
[a]Variables expressed in logarithmic values.

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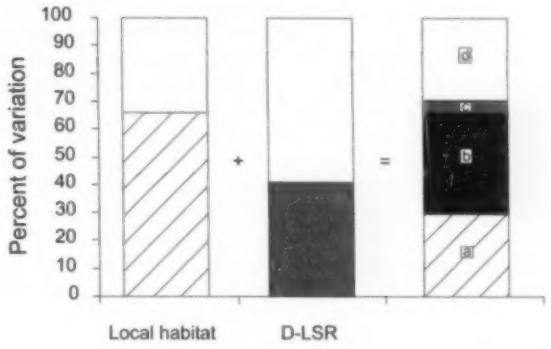
Table 5. Comparison of least-squares fits for upstream (ORDER, LINK, and AREA) and downstream (D-ORDER, D-LINK, and D-LSR) variables and local species richness (LSR) and residuals from model 1.

	Parameter	*F* ratio	*P*	R^2
LSR	ORDER	337.324	<0.0001	0.535
	LINK[a]	320.584	<0.0001	0.522
	AREA[a]	272.219	<0.0001	0.482
	D-ORDER	150.857	<0.0001	0.341
	D-LINK[a]	158.708	<0.0001	0.352
	D-LSR	201.380	<0.0001	0.408
Residuals	ORDER	1.923	1	0.007
from model 1	LINK[a]	1.081	1	0.004
	AREA[a]	0.074	1	0.001
	D-ORDER	5.082	0.150	0.017
	D-LINK[a]	1.979	0.966	0.007
	D-LSR	32.010	<0.0001	0.099

Note: Given are *F* ratio, Bonferroni probabilities (*P*), and R^2.
[a]Variables expressed in logarithmic values.

Fig. 4. Percentages of variation of local species richness (LSR) explained by local habitat conditions and by downstream local species richness (D-LSR). Separate analyses (two left-hand columns) and total variation partitioning (right-hand column) are shown. (*a*) Local habitat; (*b*) local habitat + D-LSR; (*c*) D-LSR; (*d*) undetermined.



dams) to fish movements and was never covered by glaciers during the Quaternary glaciations (Changeux and Pont 1995). Therefore, the Upper Saône basin is homogeneous from a biogeographical viewpoint: fish species remained almost free to move throughout the river network, and historical factors are unlikely to explain current patterns of fish species richness at this spatial scale.

We know of no study explicitly testing fish species richness against both local habitat and spatial factors at a similar spatial scale. Nevertheless, our results confirm earlier findings that LSR increases with stream size, but it also appears that this relationship is not linear. Among the different local habitat variables, stream width and gradient significantly influenced LSR, but spatial factors also influenced the within-basin distribution of LSR and resulted in spatial autocorrelation among sites from 4th- to 7th-order streams. This suggests that the relative importance of local habitat and spatial factors may depend on the position along the longitudinal gradient.

Longitudinal pattern in local species richness

Our results show that fish assemblages of the Upper Saône basin follow the general pattern of river fish distribution in that local species richness increases with stream order. The stream order system, traditionally used to classify lotic systems as estimator of stream size (Strahler 1957), was introduced to fish ecology by Kuehne (1962) and has since been frequently used as a framework for variation in fish assemblages along the upstream–downstream gradient (Matthews 1998). Thus, the relationship between fish species richness and stream order has been widely assessed and largely discussed (e.g., Matthews 1986), and different patterns have been revealed. As suggested by the river continuum concept (Vannote et al. 1980), fish species richness may peak and then decline with increasing stream size. Such a decline has been observed in highly regulated large European rivers and could be due to anthropogenic disturbances affecting habitat diversity (i.e., the loss of natural lotic habitats in the lowermost reaches of the Seine River; Oberdorff et al. 1993). However, Pont et al. (1985) suggested that this decline was no more apparent when highly modified sites are excluded from the analyses. Thus, the bell-shaped pattern is not a general rule for European systems, and many studies have documented a continuous longitudinal increase in fish species richness. Some authors have described linear increases in fish species richness with stream order (e.g., Naiman et al. 1987), whereas others have noted that changes in stream order do not necessarily result in abrupt changes in fish assemblage structure (Matthews 1986).

In this study, fish species richness exhibited a nonlinear relationship with stream order, clearly partitioning the river network into two parts: tributaries (1st- to 5th-order streams) and main channels (6th- and 7th-order streams). This result is consistent with the results of other studies showing that (*i*) species assemblages could differ as much within as between stream orders (e.g., Stewart et al. 1992) and (*ii*) fish species obviously respond to local habitat features, not to stream classification schemes of humans (Matthews 1998). Some authors have therefore called into question the utility of stream order and recommended the use of more measurable variables (e.g., Hughes and Omernick 1983).

Determinants of LSR

Both instream habitat characteristics and allogenic processes influence stream communities, and previous studies emphasized the role of geomorphology and riparian vegetation on the functional structure of stream communities. For example, Maridet et al. (1998) examined the relative importance of these two control factors on trophic structure of stream fish assemblages. These authors showed that riparian vegetation could be of first importance when anthropogenic alteration of riparian vegetation was severe, whereas stream fish assemblages were mainly structured by geomorphological control under natural conditions.

Here our study focused on instream processes, and geomorphological, physical, and chemical variables were used to explain fish spatial distribution. We showed that among local habitat factors, only stream width and gradient significantly influenced LSR and that no effect of stream order was apparent after having removed the effects of these two surro-

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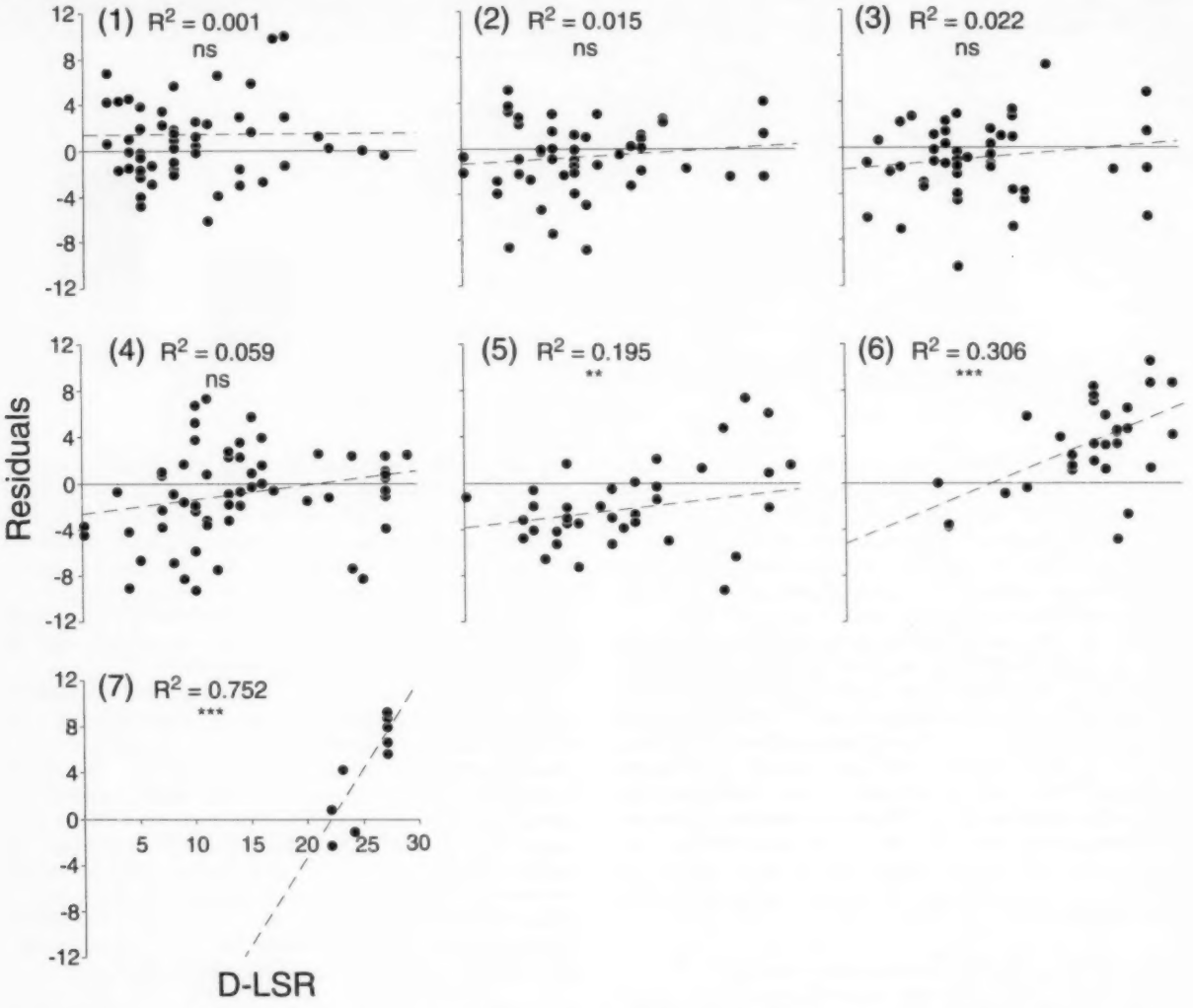
Fig. 5. Relationship between residuals from model 1 and downstream local species richness (D-LSR) for each stream order (stream order in parentheses). Broken lines represent the regression line for the stream order, with R^2 and probability P (ns, not significant; **, $P < 0.01$; ***, $P < 0.001$).



gates of stream size. This result is consistent with the results of many studies concluding that stream size was the most important factor influencing fish species composition (e.g., Matthews and Robison 1988). Note, however, that we selected significant variables using a forward-selection procedure in which variables enter the analysis by decreasing additional explanatory power. In this way, variables that could be significantly related in isolation to LSR could consequently appear nonsignificant once correlated variables were incorporated in the model. In our study, water quality, mean temperature, and thermal amplitude were all significantly and negatively correlated with stream gradient. Therefore, this could explain why neither water quality nor temperature significantly influenced LSR.

Concerning upstream and downstream influences on LSR, our results can be discussed in the light of those of Osborne and Wiley (1992), who first assessed spatial factors likely to influence fish species richness. In their study, Osborne and Wiley (1992) showed that the link magnitude of the next downstream confluence (D-LINK) accounted for the greatest proportion of variance in species richness among stations. They stressed that downstream processes could significantly influence the structure of stream fish assemblages and that the extinction–immigration hypothesis appeared to be the most plausible mechanism for the observed pattern in fish assemblage structure within a catchment.

In our study, and after removing the effect of local habitat, only local species richness of the next downstream site (D-LSR) significantly influenced LSR. This result confirms the findings of Osborne and Wiley (1992) that downstream processes can significantly influence the structure of stream fish assemblages. However, our study did not confirm Osborne and Wiley's (1992) predictions that headwater streams entering large rivers directly should have greater species richness.

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In our study, downstream influence was not apparent for smaller streams, only for larger ones. Consequently, our study not only clearly highlights spatially contagious processes in structuring stream fish assemblages, but also reveals that these processes only become significant downstream.

Biotic processes may explain variations in fish assemblage structure not explained by environmental differences among sites, and spatial autocorrelation may be interpreted as a reflection of the relative importance of biotic processes in structuring lotic communities (Wilkinson and Edds 2001). In assessing spatial autocorrelation of the Spring River basin fish assemblage, Wilkinson and Edds (2001) suggested that contagious biotic processes were important in structuring the fish assemblage. Our study reveals that the relative importance of both local habitat and spatial factors varies with the location within the river network. This is consistent with the classical view on biotic versus abiotic controls in lotic systems (e.g., Power et al. 1988) that abiotic factors are predominant upstream, whereas biotic factors are more likely to occur downstream.

Potential mechanisms responsible observed patterns

Although it was not the aim of our study to test the different mechanisms potentially responsible for the within-basin patterns in fish species richness, we can examine the different mechanisms currently invoked. Among these potential mechanisms, the importance of immigration and extinction dynamics in structuring stream fish assemblages has been underlined in a number of studies (e.g., Angermeier and Schlosser 1989; Gotelli and Taylor 1999*b*; Taylor and Warren 2001).

The fact that our results emphasize the importance of stream size in structuring stream fish assemblages can be interpreted in the light of these dynamics of immigration and extinction. Stream size has been considered as an estimator of habitat complexity (Gorman and Karr 1978) and stability (Schlosser 1987), which both have been shown to be crucial in structuring stream fish assemblages (e.g., Horwitz 1978; Angermeier and Schlosser 1989). Taylor and Warren (2001) revealed that stream size was positively correlated with immigration rates and negatively correlated with extinction rates, and they successfully attempted to relate the variability of the flow regime to the dynamics of immigration and extinction. They suggested that larger streams, characterized by larger habitats and therefore higher species richness, have a greater number of potential colonists than upstream areas. Therefore, immigration and extinction rates vary predictably along the stream gradient, and the stream-fish distribution can reflect spatial gradients in colonization and extinction probabilities (Gotelli and Taylor 1999*a*; Taylor and Warren 2001). To date, separating the relative effects of habitat heterogeneity and solely biotic processes remains challenging because very few studies have addressed how immigration and extinction rates vary along environmental gradients. Further investigations are now needed to generalize these first results to a variety of systems.

Implications

Because the location of a stream in a river network can significantly affect the number of local fish species, Osborne and Wiley (1992) recommended that managers take into account spatial influences when evaluating species richness and assemblage structure measurements. This has already been emphasized by Fausch et al. (1984), who proposed that samples from tributaries close to their confluence with larger rivers of higher stream order should be excluded from analyses when calculating index of biotic integrity (IBI) scores. However, to date, a quantitative rule for exclusion of such samples remains to be established.

Since Fausch et al. (1984), other studies have stressed the necessity of taking into account spatial influences. For example, Hinch et al. (1994) revealed that fish–habitat relationships were dramatically modified after spatial autocorrelation of sites was considered, suggesting that spatial autocorrelation may strongly affect inferences about large-scale distributional patterns. It appears from our study that spatial autocorrelation can be of major importance in the determination of local species richness. Such results are a warning for managers against neglecting spatial autocorrelation when assessing the sustainability and biological integrity of stream systems.

To provide a more comprehensive view of fish distribution patterns, some authors have attempted to use ecological attributes (or species traits) to explain within-drainage fish assemblage structure. This has been done with reproductive or trophic guilds (Oberdorff et al. 1993; Belliard et al. 1997) and revealed that the longitudinal trends in functional fish feeding groups followed the predictions of the river continuum concept (i.e., a transition from insectivorous to omnivorous and piscivorous species from headwaters to large rivers). It now seems necessary to take into account other ecological attributes of fish species, especially biological traits associated with fish colonization abilities. Indeed, differences among species in their potential to use or move among habitat patches may be critical (Matthews 1998), and some authors have recently stressed the necessity to consider variables related to dispersal success, which can dramatically affect interpretations of spatially explicit population models (e.g., Dunham and Rieman 1999).

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The wave-drag hypothesis: an explanation for size-based lateral segregation during the upstream migration of salmonids

Nicholas F. Hughes

Abstract: During their spawning migration, large salmon, e.g., chinook (*Oncorhynchus tshawytscha*), swim upstream further from the bank than smaller ones, e.g., sockeye (*Oncorhynchus nerka*). This pattern is counterintuitive because natural selection should favor behavior that minimizes migration costs, yet by traveling further from the bank, large fish will have to swim against faster currents. Existing theory predicts that they will expend more energy than necessary as a result. One explanation for this apparently paradoxical behavior is that large fish swim further from the bank to avoid wave drag, the resistance associated with the generation of surface waves when swimming close to the surface. Wave drag was incorporated into existing theory, and the resulting model was tested to determine whether it explained size-based lateral segregation of chinook and sockeye salmon in the Nushagak River, Alaska. The wave-drag model accurately predicted the migration corridor for both species. Existing theory worked well for sockeye but not for chinook. The key to these predictions is that wave drag scales according the ratio of maximum body diameter to submergence depth, so bigger fish need to swim deeper to escape its effects.

Résumé : Durant leur migration de fraye, les grands saumons, tels que le saumon quinnat (*Oncorhynchus tshawytscha*), nagent vers l'amont plus loin des berges que les petits saumons, comme le saumon rouge (*Oncorhynchus nerka*). Ce phénomène semble être contre-intuitif car la sélection naturelle devrait favoriser les comportements qui minimisent les coûts de la migration, alors que les gros poissons doivent faire face à des courants plus rapides en nageant plus loin des berges. Les théories actuelles prédisent qu'en fin de compte, ils dépenseront plus d'énergie que nécessaire. Une explication pour ce comportement apparemment paradoxal est que les gros poissons nagent plus loin de la berge pour éviter la traînée due aux vagues, soit la résistance associée à la formation de vagues de surface lorsque les poissons se déplacent près de la surface. L'incorporation de la traînée due aux vagues à la théorie actuelle a permis de vérifier si le modèle qui en résulte peut expliquer la ségrégation latérale en fonction de la taille des saumons quinnat et des saumons rouges dans la rivière Nushagak en Alaska. Le modèle de traînée due à la vague prédit de façon précise la position du corridor de migration des deux espèces. La théorie actuelle est adéquate pour le saumon rouge, mais non pour le saumon quinnat. Le point important de ces prédictions est que la traînée due à la vague croît en fonction du rapport du diamètre maximal du corps sur la profondeur de submersion. Ainsi, les poissons plus grands doivent nager en eau plus profonde pour échapper à ces effets.

[Traduit par la Rédaction]

Introduction

Sonar biologists involved in estimating the abundance of Pacific salmon during their upstream spawning migration know that larger fish tend to migrate upstream further from the bank than smaller ones. For example, chinook salmon (*Oncorhynchus tshawytscha*) generally swim further from the bank than sockeye salmon (*Oncorhynchus nerka*), and large chinook tend to swim further from the bank than small chinook (Miller 2000; Fig. 1). This pattern of behavior is so striking that biologists use distance from the bank as an important criterion when determining whether an acoustical target is a sockeye or a chinook (Steve Fleischman, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, Alaska, personal communication).

No one has yet attempted to explain this size-based lateral segregation, but the pattern seems rather counterintuitive. We might expect natural selection to favor behavior that minimizes the cost-per-unit-distance of travel during migration, yet by swimming upstream further from the bank, larger fish will have to make headway against faster currents, even if they swim near the streambed. Existing theory on the cost of upstream migration predicts that they will expend more energy than necessary as a result (e.g., Brett 1995; Webb 1995; Hinch and Rand 2000).

One explanation for this paradoxical behavior is that large fish swim upstream further from the bank than small ones to avoid wave drag. Wave drag is the resistance that results from the generation of surface waves when a fish moves close to the air–water interface. Hertel (1966) provides a figure showing that wave drag can be substantial, up to four times the drag that a fish experiences when swimming well submerged (Hertel's figure has been reproduced in at least three books on fish swimming: Webb (1975), Blake (1983*a*),

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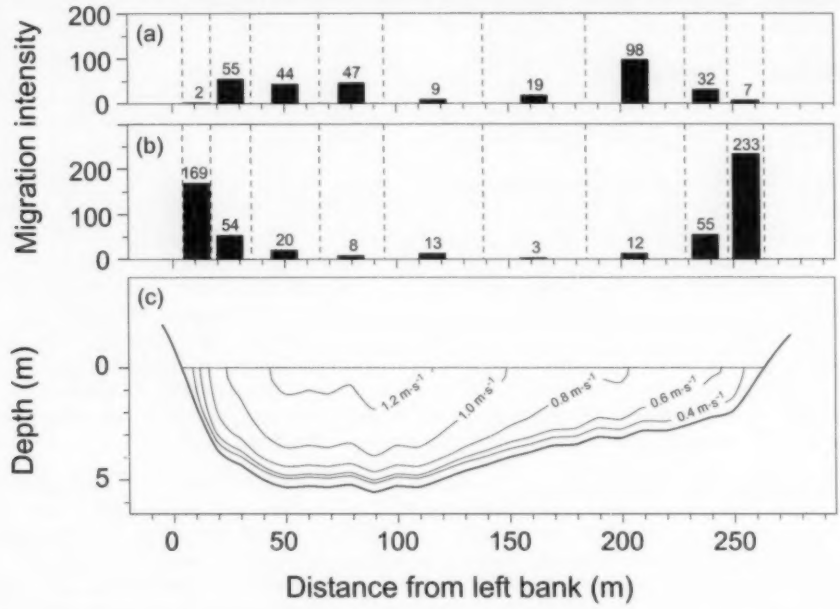
Fig. 1. Lateral distribution of (*a*) chinook (*Oncorhynchus tshawytscha*) and (*b*) sockeye (*O. nerka*) salmon in relation to (*c*) water depth and simulated water velocity contours as they migrate past a site on the Nushagak River. In (*a*) and (*b*), for each species, the relative abundance of fish passing through each of nine subsections is expressed as migration intensity, an estimate of the number of migrants per metre of cross section per 10 000 migrants. Note that the width of the nine sections varies, as shown by the vertical broken lines. Based on the gill-net catch-per-unit-effort data, cross-sectional profile, and stage-discharge relationship reported by Miller (2000).



and Videler (1993)). Hertel's figure shows that the magnitude of wave drag depends on the ratio of submerged depth to maximum body diameter; therefore, big fish need to swim deeper to escape its effects. As a consequence, it may be more economical for large fish to swim further from the bank than small ones because the extra cost of swimming against faster water is offset by a reduction in wave drag.

The purpose of this paper was to incorporate the wave-drag hypothesis into existing models predicting the swimming speed and cost-per-unit-distance of travel during upstream migration and to determine if the resulting model explains why big fish swim further from the bank than small ones.

Existing theory and the wave-drag model

Existing theory of salmon migration assumes that fish will swim upstream at the speed that minimizes the cost-per-unit-distance of travel (e.g., Brett 1995; Webb 1995; Hinch and Rand 2000). For any water velocity, the cost-minimizing speed can be found by plotting the cost-per-unit-time against swimming speed and then drawing a line that passes through the point on the x axis corresponding to the current speed and tangent to the cost curve (Fig. 2*a*). The point at which this line touches the cost curve corresponds to the cost-minimizing swimming speed on the x axis (relative to the water) and the cost-per-unit-time for migrating at this speed on the y axis. Subtracting water velocity from the cost-minimizing swimming speed gives the cost-minimizing ground speed and dividing cost-per-unit-time by the cost-minimizing ground speed gives the cost-per-unit-distance traveled. This simple model is illustrated using Brett and Glass' (1973) method of estimating the relationship between fish size, water temperature, swimming speed, and swimming costs (SC; Fig. 2*a*). The relationship between swimming speed and swimming cost is described by the following equation:

$$(1) \qquad SC = e^{\ln(SMR)+u\frac{\ln(AMR)-\ln(SMR)}{ucrit}}$$

where SMR is the fish's standard metabolic rate and AMR is the fish's active metabolic rate (both in mg $O_2 \cdot kg^{-1} \cdot h^{-1}$); ucrit is the fish's maximum sustainable swimming speed and u is the swimming speed of interest (both in $m \cdot s^{-1}$). SMR, AMR, and ucrit were estimated using the equations developed by Hughes and Kelly (1996) to duplicate the contour maps of these variables provided by Brett and Glass (1973). When necessary oxygen consumption was converted to joules using an oxycaloric equivalent of 14.1 J·mg O_2^{-1} (Videler 1993).

This theory has been used to predict the cost of swimming upstream against a specified current velocity (e.g., Hinch and Rand 2000) but not, to my knowledge, to predict migration corridors. I adapted this theory to predict migration corridors simply by assuming that fish will use the migratory corridor that minimizes the cost of upstream migration. For convenience, this approach is termed the traditional model.

To extend this model to account for the added resistance that a fish experiences when swimming near the surface, we need to incorporate a relationship between submergence depth and the severity of wave drag. This can be done by using the figure provided Hertel (1966) to estimate the total re-

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Fig. 2. A graphical technique for estimating the swimming speed, $uopt_w$, that minimizes the cost-per-unit-distance of upstream travel for a 2.5-kg sockeye (*Oncorhynchus nerka*) at 10 °C (*a*) in the absence of wave drag and (*b*) with the wave drag appropriate to a fish swimming 0.29 m beneath the surface. Swimming cost curves are calculated with eqs. 1 and 2, respectively; $uopt_g$ is the fish's ground speed at $uopt_w$. In (*b*), the cost curve for swimming without wave drag is reproduced as a broken line to show how the wave-drag model increases the costs associated with locomotion, but not standard metabolic rate.

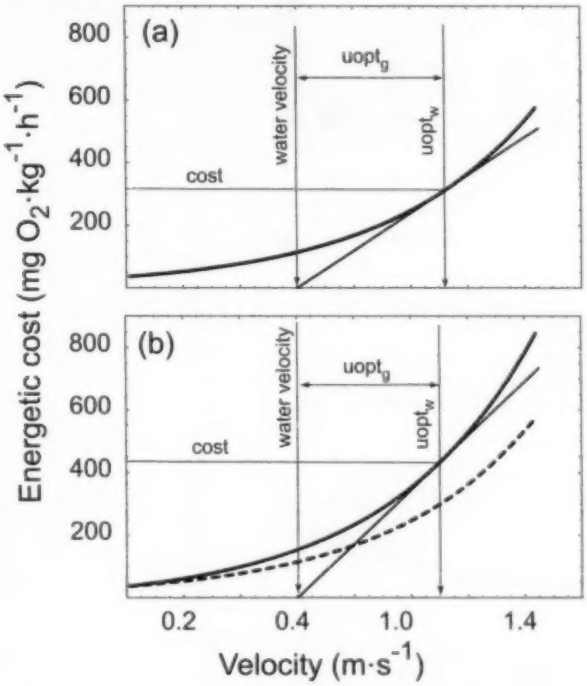
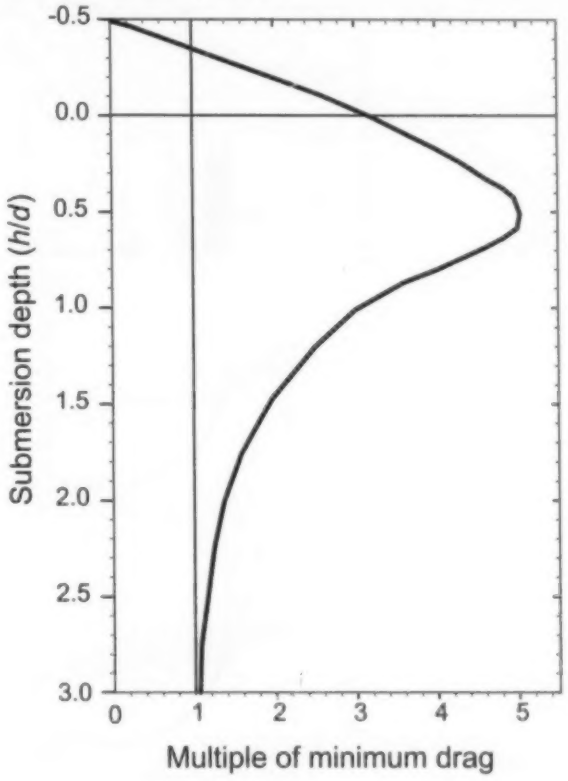


Fig. 3. Relationship between submersion depth and total drag on a streamlined body of rotation. Based on fig. 289 in Hertel (1966). Submersion depth is expressed as *h*/*d*, where *h* is the distance of the midline of the body from the surface of the water and *d* is maximum body diameter.



sistance experienced by the fish as a multiple of the drag that it would experience when swimming more than three body diameters beneath the surface (Fig. 3). In accordance with Hertel's plot, this multiple (TR) will be 1 when the fish is swimming more than three body diameters beneath the surface and will peak at about 5 when the fish is swimming just ½ body diameter beneath the surface. The fish's swimming cost can then be estimated using a modification of eq. 1:

$$(2)\qquad SC = SMR + TR(e^{\ln(SMR)+u\frac{\ln(AMR)-\ln(SMR)}{ucrit}} - SMR)$$

This equation multiplies just the cost of swimming over and above SMR by TR to provide a model that accounts for the effects of both water velocity and submergence depth on the cost of upstream migration (Fig. 2*b*).

Testing the wave-drag model

To test whether the wave-drag model explains size-based lateral segregation better than the traditional model, both approaches were used to predict the location of cost-minimizing migration corridors for sockeye and chinook in the Nushagak River, Bristol Bay, Alaska. These predictions were then compared with the migration paths actually favoured by the two species (Miller 2000).

Velocity distribution was predicted at a site on the Nushagak River during early July 1999 using equations from Gordon et al. (1992) and Miller's (2000) data on the cross-sectional profile, water depth, and discharge. Mean water velocity was estimated at 1-m intervals across the channel as $\bar{v} = 1/n \cdot r^{2/3} \cdot s^{1/2}$, where Manning's n is $0.013d^{1/6}$, mean bed particle diameter, d, is 150 (mm), and the hydraulic radius, r, is approximated by water depth (m). A channel slope, s, of 0.000181 was selected to produce the observed discharge of 950 $m^3 \cdot s^{-1}$. Vertical velocity profiles were simulated assuming that water velocity, v, was zero at the streambed and varied according to the relationship $v = (5.75v^* \cdot \ln(30y/k)/2.30$, where the shear velocity, v^*, is $0.40\,\bar{v}/\ln(12.3r/k)$, y is distance from the streambed (m), and k is the roughness height 0.15 (m).

The location of the minimum-cost migration corridor was determined by using each model to calculate the cost-per-unit-distance of migrating upstream at various points on the cross section for a 2.5-kg sockeye and a 25-kg chinook, assuming a water temperature of 10 °C. The migration corridor was restricted by assuming that fish must swim at least

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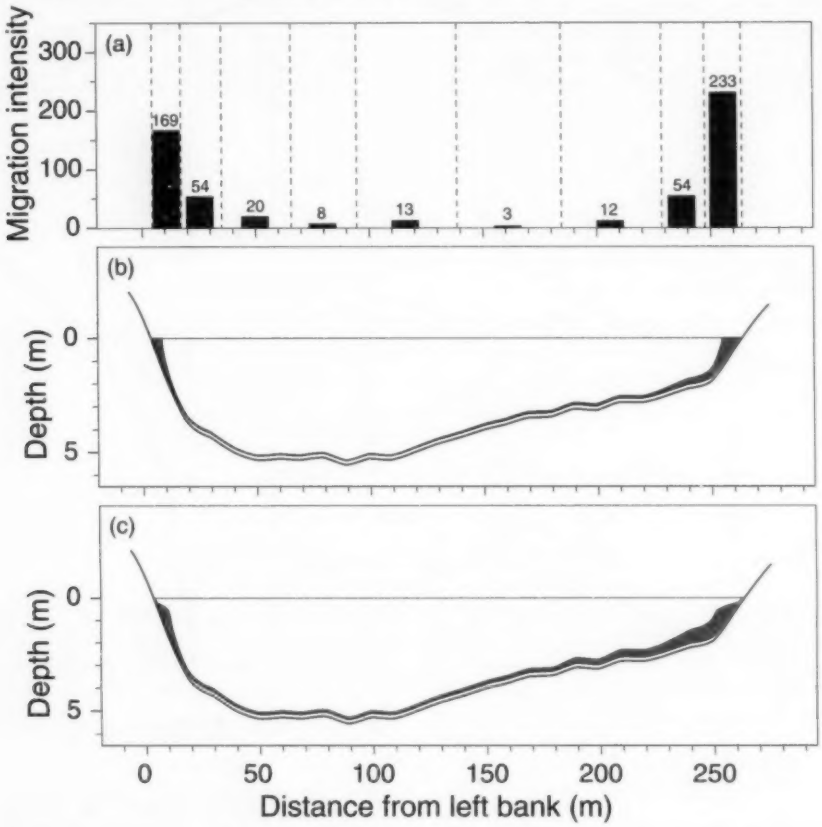
Fig. 4. (*a*) Observed lateral distribution of sockeye salmon (*Oncorhynchus nerka*) in the Nushagak River and predicted cost-minimizing migration corridors under (*b*) the traditional model and (*c*) the wave-drag model. The shaded area shows that part of the cross section in which the cost-per-unit-distance travelled is no more than twice the minimum cost available to the fish. In (*a*), the relative abundance of fish passing through each of the nine subsections is expressed as migration intensity, an estimate of the number of migrants per metre of cross section per 10 000 migrants. Note that the width of the nine sections varies, as shown by the vertical broken lines. Based on the gill-net catch-per-unit-effort data reported by Miller (2000).



1 body diameter from the streambed to avoid scraping the bottom. Maximum body diameter was estimated as 0.3·length, and fish length (m) was estimated from weight (g) using an equation from Brett and Glass (1973), length = $10^{(0.71+0.32\log_{10}(\text{weight}))}/100$. Estimated body depth was 0.18 m for sockeye and 0.38 m for chinook. The minimum-cost migration corridor was defined as that part of the cross section in which the cost-per-unit-distance travelled is no more than twice the minimum available cost.

The results of these simulations are shown in Figs. 4 and 5. If the relative vertical depth of the minimum-cost migration corridor is a reasonable index of its quality, then the wave-drag model is better at explaining size-based lateral segregation than the traditional model. The difference between the two models is well illustrated by the three sections closest to the right bank of the river, which span a total of 80 m. The traditional model predicts that the depth of the migration corridor will decrease with increasing distance from the shore for both species. In contrast, the wave-drag model predicts that the thickness of the corridor will decrease with increasing distance from the bank for sockeye but increase for chinook. The observed trend of decreasing sockeye abundance and increasing chinook abundance with increasing distance from the bank fits the predictions of the wave-drag model, not the traditional model. The same pattern holds true for the two sections closest to the left bank, but over a smaller distance of only 30 m.

The wave-drag model also comes out on top when we compare the ability of the two models to predict the section that each species will prefer. If we assume that fish will prefer the section where the migration corridor has the greatest mean depth, then the wave-drag model predicts the correct sections for both species on both banks. Chinook should prefer the second section from the bank on the left and the third section from the bank on the right, and in fact these are the two sections most commonly used. The traditional model predicts that chinook should swim too far inshore, using the most inshore section on the left and the second section from the bank on the right. Both models correctly predict that sockeye should prefer the most inshore sections along both banks. If we divide the river into four sections to the left of the thalweg and five to the right, the binomial test shows that the probability of getting predictions as accurate as the wave-drag model by chance is 0.05 for each species consid-

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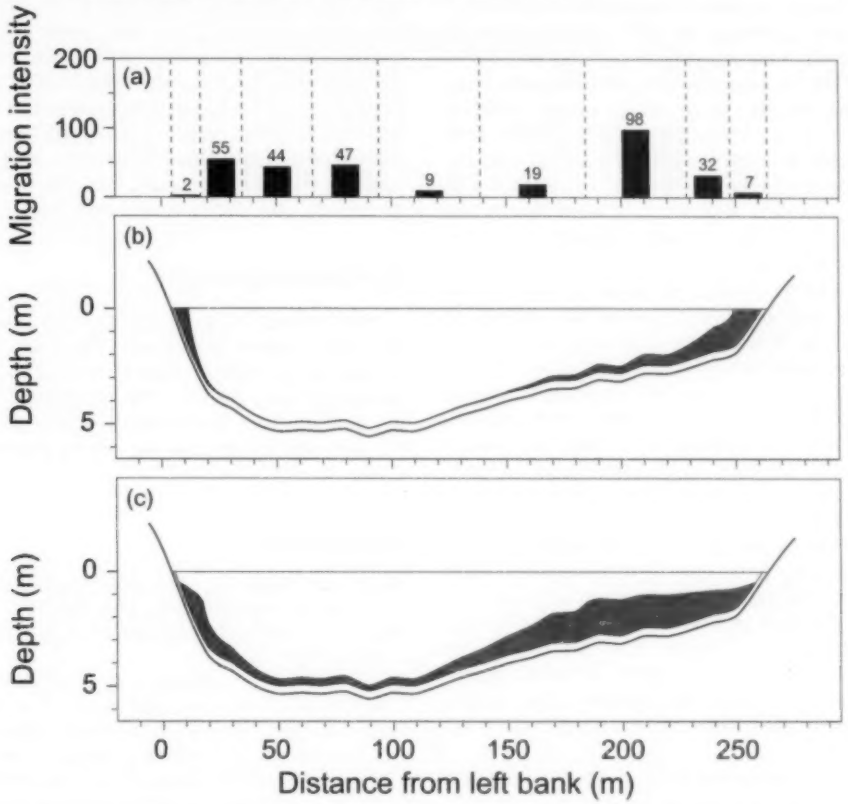
Fig. 5. (*a*) Observed lateral distribution of chinook salmon (*Oncorhynchus tshawytscha*) in the Nushagak River and predicted cost-minimizing migration corridors under (*b*) the traditional model and (*c*) the wave-drag model. The shaded area shows that part of the cross section in which the cost-per-unit-distance travelled is no more than twice the minimum cost available to the fish. In (*a*), the relative abundance of fish passing through each of the nine subsections is expressed as migration intensity, an estimate of the number of migrants per metre of cross section per 10 000 migrants. Note that the width of the nine sections varies, as shown by the vertical broken lines. Based on the gill-net catch-per-unit-effort data reported by Miller (2000).



ered separately and 0.0025 for both species together. For the traditional model, the probabilities are 0.05 for sockeye alone, 0.6 for chinook alone, and 0.16 for both species together. This demonstrates that although either model can explain why sockeye swim near the banks, the wave-drag model is better at explaining why chinook swim further from the bank, and it gives a more comprehensive explanation for lateral segregation.

If fish conform to the wave-drag model rather than the traditional model, they will swim against faster water, swim faster, maintain the same ground speed, and pay a higher energetic cost for migration. Assuming that fish are equally likely to select any route within the predicted migratory corridor, the mean water velocity faced by sockeye in the Nushagak would increase 14%, from 0.51 $m \cdot s^{-1}$ under the traditional model to 0.58 $m \cdot s^{-1}$ under the wave-drag model, average swimming speed would increase 8%, from 1.02 to 1.10 $m \cdot s^{-1}$, average ground speed would remained constant at 0.52 $m \cdot s^{-1}$, and average energetic costs would increase 15%, from 5.0 to 5.7 $J \cdot m^{-1}$, or from 2.6 to 2.9 $J \cdot s^{-1}$. For chinook, comparable figures were as follows: an increase in water velocity of 14%, from 0.76 to 0.88 $m \cdot s^{-1}$; an increase in average swimming speed of 7%, from 1.55 to 1.65 $m \cdot s^{-1}$, a constant average ground speed of 0.78 $m \cdot s^{-1}$, and an increase in energetic costs of 18%, from 25.4 to 29.9 $J \cdot m^{-1}$, or from 19.8 to 23.3 $J \cdot s^{-1}$.

Discussion

The wave-drag hypothesis can explain why large fish such as chinook salmon swim upstream further from the bank than smaller ones such as sockeye. It also makes better predictions of the fish's migratory corridor than the traditional model. The wave-drag model predicts that larger fish will swim upstream further from the bank because the minimum-cost migration corridor moves offshore as fish size increases. Fish that use this corridor optimize the trade-off between swimming in deeper faster water to reduce wave drag and swimming in shallower slower water to reduce skin friction and form drag. Compared with the traditional model, the wave-drag hypothesis predicts that fish will swim against faster water and pay higher energetic costs to migrate.

Perhaps the most surprising aspect of the wave-drag hypothesis is that although the importance of wave drag has been known for years (e.g., Hoerner 1965; Hertel 1966), it has been neglected by biologists interested in salmon migra-

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tion and, for that matter, by practically everyone interested in fish swimming near the air–water interface. The only experimental study that addresses its importance to fish is Webb et al.'s (1991) investigation of the effect of wave drag on the fast start performance of rainbow trout (*Oncorhynchus mykiss*). Reassuringly, they found that Hertel's (1966) curve provided a rather close fit to their experimental data; in shallow water, wave drag accounted for 80% of the total resistance to acceleration. On the theoretical side, Au and Weihs (1980) and Blake (1983*b*) examined the possibility that leaping by marine mammals may be an energy-saving behavior designed, in part, to avoid wave drag. Blake (1983*b*) used Hertel's (1966) figure in a very similar manner to that described in this paper except, following Au and Weihs (1980), he restricted the drag multiple to no more than 4.5 to account for the fact that fish and marine mammals are not perfect bodies of revolution.

It would not be hard to criticize the model presented here for lack of realism, both in its treatment of fish swimming and flow modeling, but at this stage simplicity might be an asset as it makes the model easier to apply. In reality, the relative importance of wave drag may not be constant, as assumed in this model, but may depend on the Froude number (the ratio of inertial to gravitational forces; see Vogel (1994)). For example, Hoerner (1965) reproduced a figure from Wigley (1953) suggesting that a plot of the relative importance of wave drag against the Froude number has two maxima; this could have some interesting biological implications. Another intriguing possibility is suggested by Tuck and Scullen's (1998) mathematical analysis of the forces acting on submerged cylinders in a flow. The spacing and submerged depth of these cylinders can result in the cancellation of wave drag, with or without attendant attractive or repulsive forces between the cylinders. Fish swimming in groups may exploit these effects, as suggested by Radakov (1973).

Based on the analysis presented here, it seems likely that wave drag plays an important part in producing size-based lateral segregation of fish during upstream migration, but it may not be the only factor involved. It is also possible that fish use velocity gradients and turbulence near the streambed in a way that is not captured in the wave-drag model. These conditions will depend on bed roughness, which typically increases towards the middle of a channel, and may make it advantageous for larger fish to swim upstream further from the bank. Hinch and Rand's (2000) discovery that fish may extract energy from vortices is relevant here. Another possibility is that big fish swim further from the bank to avoid their principle terrestrial predator, the brown bear (*Ursus arctos*). However, bear avoidance is unlikely to be the primary cause of the pattern because lateral segregation is found in large rivers, some highly turbid with glacial silt, where bears are not effective predators. In fact, the risk of predation may be greatest in deep water because the important aquatic predators, beluga whales (*Delphinapterus leucas*) and harbour seals (*Phoca vitulina*), are probably more effective there.

These considerations of piscivory bring attention to an important aspect of wave drag. Because it scales with the ratio of submerged depth to maximum body diameter, small fish can avoid its effects while swimming closer to the surface than their larger predators. This may give small fish an advantage in shallow water and have important consequences for habitat selection and swimming behavior of both predators and prey, as noted by Webb et al. (1991). An extreme example of near-surface predator–prey interactions is provided by flying fish, Exocoetidae, which exploit the physics revealed in Hertel's (1966) plot to the full by gliding above the water, where drag is vastly lower than for any predator pursuing them below the surface. The slender bodies and frequent leaps of some piscivores, e.g., needlefishes (Belonidae), may also be adaptations to reduce wave drag as they pursue their prey near the surface. These examples show that the wave-drag hypothesis suggests new ways of looking at almost any aspect of fish ecology that involves swimming near the air–water interface.

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Variation in neutral and polar lipid compositions of ova in ten reproductively isolated populations of walleye (*Sander vitreus*)

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Abstract: We examined variation in the mass and composition of egg lipids within and among 10 walleye (*Sander vitreus*) populations. Larger eggs contained more lipid, but neither absolute lipid content (mg·egg^{-1}) nor relative lipid content (percent of egg mass as lipid) were related to maternal age or size. Among populations, the proportion of egg mass as neutral lipid varied significantly, whereas the proportion as polar lipid did not. Egg fatty acid composition did vary with respect to maternal traits. In the Lake Ontario population, larger females appear to produce a qualitatively superior egg; relative abundances of docosahexaenoic acid (22:6(*n*–3), DHA) and arachidonic acid (20:4(*n*–6), AA) increased, and the relative abundance of eicosapentaenoic acid (20:5(*n*–3), EPA) decreased in egg fatty acids with increasing maternal length. We predicted that fatty acid profiles would be less variable in the polar than in the neutral lipid fraction. Relative abundances of DHA, AA, the sum of AA and EPA, and several other fatty acid classes were all significantly less variable in the polar than in the neutral fraction both among females and among populations. Our results indicate a high level of conservatism of egg lipid mass and polar lipid composition in this species.

Résumé : Nous avons déterminé la variation de la masse et de la composition des lipides des oeufs du doré jaune (*Sander vitreus*) au sein de 10 populations, ainsi qu'entre les populations. Les oeufs les plus grands contiennent plus de lipides, mais ni le contenu absolu (mg/oeuf), ni le contenu relatif (pourcentage de la masse de l'oeuf représenté par les lipides) de lipides ne sont reliés à l'âge ou à la taille de la mère. D'une population à l'autre, le pourcentage de la masse des oeufs composé de lipides neutres varie de façon significative, mais non le pourcentage de lipides polaires. La composition en acides gras des oeufs varie avec les caractéristiques de la mère. Dans la population du lac Ontario, les femelles plus grandes semblent produire des oeufs de qualité supérieure: les abondances relatives des acides docosahexaénoïque (22:6(*n*–3), DHA) et arachidonique (20:4(*n*–6), AA) augmentent et l'abondance relative de l'acide eicopentaénoïque (20:5(*n*–3), EPA) diminue parmi les acides gras des oeufs en fonction de la longueur de la femelle. Nous avons prédit que les profils d'acides gras devraient être moins variables dans la fraction des lipides polaires que celle des lipides neutres. Les abondances relatives de DHA, d'AA, de la somme d'AA et d'EPA, ainsi que de plusieurs autres classes d'acides gras sont toutes significativement moins variables dans la fraction polaire que dans la fraction neutre, tant parmi les femelles qu'entre les populations. Nos résultats indiquent un fort degré de conservatisme de la masse lipidique des oeufs et de la composition en lipides polaires chez cette espèce.

[Traduit par la Rédaction]

Introduction

The lipid reserve in teleost fish eggs provides structural materials, micronutrients, and a source of catabolic substrate for developing embryos. The essential fatty acids (EFA) of the (*n*–3) and the (*n*–6) series are especially important.[3] They are not known to be synthesized de novo by vertebrates, and many fish cannot produce adequate amounts of the longer chain (*n*–3) or (*n*–6) fatty acids from C18 precursors (Sargent et al. 1999*a*). Among the (*n*–3) fatty acids, docosahexaenoic acid (22:6(*n*–3), DHA) is found in particularly high concentrations in brain and retinal polar lipids (Bell and Dick 1991; Bell et al. 1996; Mourente et al. 1999). Deficiencies in this fatty acid result in impairment of larval behaviours (Bell et al. 1995; Masuda et al. 1998; Ishizaki et al. 2001) and brain growth (Ishizaki et al. 2001). The C20 EFAs, arachidonic acid (20:4(*n*–6), AA) and eicosapentaenoic acid (20:5(*n*–3), EPA), both serve as precursors for eicosanoids. The ratio of

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[3]Fatty acids are designated *a*:*b*(*n*–*x*), where *a* is the number of carbon atoms, *b* is the number of methylene-interrupted double bonds, and (*n*–*x*) indicates the position of the first double bond relative to the methyl end of the molecule.

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these two fatty acids in tissues has been found to influence physiological function and overall viability (Sargent et al. 1995, 1999*a*, 1999*b*). Both AA and EPA are also important in vertebrate structural phospholipids, including those of fish (Bell and Dick 1991; Dey et al. 1993). Requirements for EFA are varied among species and are influenced by life history (Sargent et al. 1999*a*).

Recent investigations of a number of species have shown that maternal diet can influence the fatty acid profile of egg lipid reserves and thereby egg quality (Fernandez-Palacios et al. 1995; Navas et al. 1997; Rodriguez et al. 1998). The fatty acid profiles of neutral lipids tend to vary more than those of polar lipids in response to manipulation of the vitellogenic female's diet (Wiegand 1996; Bell et al. 1997; Almansa et al. 1999). These observations could be explained by a tighter regulation of the composition of the polar lipid portion of the egg nutrient reserve.

In contrast, little is currently known about the magnitude and character of variability in egg fatty acid profiles within and among wild fish populations. This is of interest because populations may differ in adult diets and, by extension, in the fatty acid requirements of their embryos.

We selected walleye (*Sander vitreus*, formerly *Stizostedion vitreum*) as our target species to examine variation in the quantity and quality of egg lipids. Walleye are piscivorous and are native to lakes and rivers over a range extending from the southern United States to the MacKenzie River delta in northern Canada (Scott and Crossman 1973). Reproductive characteristics vary considerably over this range (Colby and Nepszy 1981). Walleye are iteroparous, and spawning takes place in early spring each year. Within populations, larger and older females generally produce more eggs (Baccante and Reid 1988) and, in some populations, larger eggs (Johnston and Leggett 2002). Egg survival can also be linked to maternal age and size (Johnston 1997). Fecundity and egg size vary substantially among populations with respect to both environmental conditions (Baccante and Colby 1996; Johnston and Leggett 2002) and changes in population density brought about by exploitation (Baccante and Reid 1988).

The lipid allocated to egg production in walleye is divided between a lipoprotein yolk (LPY), which contains polar lipids and some neutral lipids, and an oil globule that consists entirely of neutral lipids, principally triacylglycerols (Moodie et al. 1989). The LPY is used to satisfy structural as well as caloric and micronutrient requirements of the embryo and young larva and is largely exhausted before the commencement of exogenous feeding (McElman and Balon 1979). The oil globule serves primarily as a caloric reserve and is utilized after the larva begins exogenous feeding (Moodie et al. 1989). The viability of walleye larvae appears to be related to the size of the egg nutrient reserve (Moodie et al. 1989) and the fatty acid profiles of both the egg and the larval diet (Czesny and Dabrowski 1998; Czesny et al. 1999). How the lipid provisioning of walleye eggs varies with respect to maternal characteristics or among populations is currently unknown.

Our objective was to explore intraspecific variation in the lipid composition and fatty acid profiles of ova in wild walleye populations. Specifically, we sought to evaluate several predictions concerning how lipid is allocated to egg production. First, we predicted that both the mass and fatty acid composition of the egg lipids would be related to maternal age and size. Previous research has indicated that egg size is related to these maternal traits in some populations (Johnston and Leggett 2002). Second, we predicted that the fatty acid profile of the polar lipid fraction would be less variable than that of the neutral fraction because of the more critical structural function of the former.

Materials and methods

Field sampling

We sampled unfertilized ova from 10 reproductively isolated walleye populations from across their native North American range (Table 1) between 1996 and 2000. Walleye spawn early in the spring when water temperatures reach 6–10 °C and therefore sampling dates ranged from early March in the south to early May in the north. Females in spawning condition (eggs ovulated and free-flowing) were sampled from known spawning sites or females in prespawn condition were captured during their spawning migration and held in mesh pens until they attained spawning condition. Within each population, females were sampled haphazardly, except with respect to body size.

For each of nine populations, we sampled six females (five in Falcon Lake) within a size range of 450- to 600-mm fork length (FL); this generally covered the middle of the observed size range. In the remaining population (Bay of Quinte, Lake Ontario), we sampled 42 females covering a much wider size range (449- to 802-mm FL) in order to assess within-population variation. Six of these 42 females ranging in size from 450- to 600-mm FL were selected for inclusion with samples from the other nine populations in interpopulation comparisons (see Statistical analyses). For each female, a sample (~30 mL) of ripe ova was stripped, body length was measured (FL, mm), and the second and third dorsal spines were removed before the fish was released. The one exception was the Lake Ontario population; ovulated females were sacrificed at capture and an opercle was removed instead of dorsal spines. Egg samples were immediately poured into plastic bags, packed on wet ice or freezer packs, and transported fresh to the laboratory.

In the laboratory, an aliquot of the fresh ova was removed for dry mass determinations. The remaining eggs were immediately frozen at –70 °C until lipid analyses were performed. Mean egg dry mass was estimated by oven drying at 60 °C and weighing subsamples of known numbers (~30) of fresh ova in preweighed glass vials (Johnston and Leggett 2002). Female ages were determined by counting annuli on sections of dorsal fin rays or by counting annuli on opercles (Campbell and Babaluk 1979).

Analytical procedures

Subsamples of ~700 mg were broken off the frozen egg mass from each female and placed immediately into chloroform–methanol (2:1 by volume) for extraction by grinding. After a second extraction, the combined extracts were pooled and washed with 0.88% aqueous potassium chloride (modified from Folch et al. 1957). Separation of neutral lipids (NL) and polar lipids (PL) was accomplished using silica gel (230–400 mesh; Sigma-Aldrich Corp., St. Louis,

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Table 1. Maternal characteristics of sampled fish (mean ± one standard deviation).

Population (latitude, longitude)	*N*	FL (mm)	Age (years)	Egg dry mass (mg)
(1) Greer's Ferry Reservoir (35°33′N, 92°25′W)	6	478±53	4.2±1.0	1.06±0.09
(2) Lake Ontario (44°0′N, 76°40′W)	6	503±35	6.2±1.0	1.02±0.05
(3) Otter Tail Lake (46°28′N, 95°45′W)	6	494±37	9.3±1.9	0.88±0.11
(4) Lake Superior (46°44′N, 92°6′W)	6	503±9	8.8±0.8	1.04±0.13
(5) Lake Winnibigoshish (47°27′N, 94°11′W)	6	503±23	6.3±0.8	0.84±0.08
(6) Vermilion Lake (47°52′N, 92°20′W)	6	504±16	8.0±0.9	0.88±0.09
(7) Lake of the Woods (49°7′N, 94°0′W)	6	499±30	5.7±0.5	0.77±0.08
(8) Falcon Lake (49°42′N, 95°17′W)	5	544±15	7.8±1.1	0.83±0.06
(9) Lake Manitoba (50°36′N, 98°7′W)	6	499±21	5.5±0.6	0.77±0.09
(10) Primrose Lake (54°54′N, 109°42′W)	6	501±5	8.8±1.3	0.76±0.05

Note: Populations are ordered from south to north. Note that only the six fish used in interpopulation comparisons are included for the Lake Ontario population. FL = fork length.

Mo.) columns. A petroleum ether (30–60 °C) slurry of silica gel was poured to a depth of 1.3 cm into a column consisting of a disposable Pasteur pipette plugged with glass wool. The gel was washed with about 5 mL petroleum ether followed by 10 mL dichloromethane–methanol (DCM-M, 19:1 by volume) containing 0.01% butylated hydroxytoluene (BHT; Sigma-Aldrich Corp.). A 2-mL aliquot of chloroform lipid extract containing approximately 10 mg total lipid was added to the column. Neutral lipids were eluted with a further 3 mL chloroform, followed by 14 mL of the DCM-M solution. Polar lipids were then eluted with 24 mL methanol, also containing 0.01% BHT. Authenticity of the fractions was routinely confirmed by thin-layer chromatography (Wiegand and Idler 1982). For each fraction, eluates were saponified in ethanolic KOH (Wiegand and Idler 1982). Fatty acid methyl esters were prepared with boron triflouride – methanol (Wiegand and Idler 1985) and analysed by gas chromatography (Moodie et al. 1989). Thin-layer chromatography was used to confirm homogeneity of the fatty acid methyl ester preparations before injection into the gas chromatograph. Generally, two or three chromatograms were generated for each sample, and mean fatty acid profiles were determined for both the neutral and polar lipid fractions of each female's eggs.

To determine lipid mass, a second subsample was taken from the frozen eggs. These were thawed slowly in distilled water and 30 eggs were counted out for extraction. Eggs of the Lake Ontario population were lyophylized before counting. An aliquot of each extract was taken for isolation of neutral lipids as described above except that the DCM-M solution did not contain BHT. Mass of total and neutral lipid was determined by charring using tripalmitin as standard (Marsh and Weinstein 1966). Total and neutral lipid mass data were then converted to walleye egg equivalents. To do this, extracts were prepared from seven samples randomly chosen from six of the populations, and neutral lipids were isolated by column chromatography. Masses of total and neutral lipid were determined both gravimetrically and in the charring assay in order to derive appropriate conversion factors. Polar lipid masses were then estimated by difference using the corrected total and neutral lipid masses.

Statistical analyses

We examined variability in the total lipid mass and relative proportion of neutral and polar lipid masses in the eggs, first among females, then among populations. Neutral and polar lipid masses were expressed on a mass per egg basis. Fatty acid profiles were generated using the 29 known fatty acids routinely found. Because there are competitive interactions among the fatty acids in metabolism, we chose to express tissue levels in relative amounts as proportions of the total fatty acids. Proportions were normalized to 100% then arcsine square root transformed before all statistical analyses. Specific fatty acids selected for analyses were the essential fatty acids (AA, EPA, and DHA) along with two other fatty acids with a prominent structural role, palmitic acid (16:0) and oleic acid (18:1(*n*–9)) (Bell and Dick 1991; Dey et al. 1993; Buda et al. 1994). We also assessed variability in the percentage abundance of total fatty acids in each of the four families: saturated fatty acids (SFA), monounsaturated fatty acids (MUFA), (*n*–6) polyunsaturated fatty acids (PUFA), and (*n*–3) PUFA along with the sum of AA and EPA (AA + EPA).

Statistical analyses of egg lipid characteristics were conducted by regression analysis, analysis of variance (ANOVA), and analysis of covariance (ANCOVA) (SAS Institute Inc. 1990). Interpopulation variability in fatty acid profiles was assessed through examination of principal components calculated from the 29 fatty acid relative abundances. We compared interpopulation variability between neutral and polar lipid fractions using coefficients of variation (CV). Standard errors of the CVs across populations were estimated by jackknifing (Efron and Gong 1983), and nonoverlapping confidence intervals for the CV means between neutral and polar fractions were interpreted as significant differences in variability.

Results

Variation within populations

We predicted that the larger and (or) older females in the Lake Ontario spawning population would produce more lipid-rich eggs. There was no significant relationship between egg mass and maternal fork length (regression analysis, $F = 0.15$, df = 1,41, $P = 0.70$, $R^2 < 0.01$) or between egg mass and maternal age ($F = 0.00$, df = 1,41, $P = 0.97$, $R^2 < 0.01$) in this population. Total lipid content (mg·egg^{-1}) increased with egg dry mass (Fig. 1), but neither maternal age nor size accounted for significant amounts of the remaining variation in total lipid content (multiple regression analysis,

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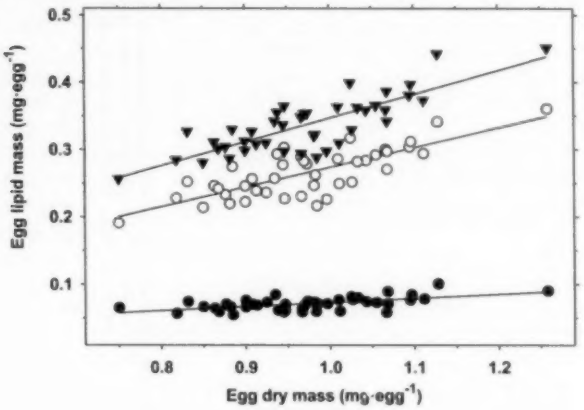
Fig. 1. Total (▼), neutral (○), and polar(●) lipid mass vs. egg dry mass for Lake Ontario walleye (*Sander vitreus*; $n = 42$ females). Lines were fitted by least-squares regression ($F > 20$, $P < 0.001$, $R^2 > 0.34$).



partial $F < 0.85$, $P > 0.36$). Residual plots confirmed that there was no clear relationship between remaining variation in total lipid content and maternal age or size. Repeating this analysis using neutral or polar lipid mass per egg as dependent variables yielded the same outcomes. Similarly, the proportion of egg dry mass as neutral or polar lipid did not vary significantly with respect to egg mass, maternal age, or maternal size (regression analysis, $F < 1.5$, $P > 0.23$). In Lake Ontario walleye, total lipid comprised 34.6 ± 2.5% (mean ± one standard deviation) of egg dry mass; the values for neutral and polar lipid were 27.3 ± 2.4% and 7.4 ± 0.8%, respectively.

We predicted that the fatty acid profile of walleye eggs would vary with respect to the age and size of the females within the Lake Ontario spawning population. Fatty acid profiles of walleye egg NL and PL in the Lake Ontario population were similar to those observed in the other nine populations (Table 2). We constructed multiple regression models in which transformed fatty acid proportions were regressed against maternal age, maternal size, and egg dry mass; nonsignificant terms were removed sequentially by backward elimination (partial F test, $P > 0.05$). Among-female variation in fatty acid profiles was most strongly correlated to maternal size measured as fork length (Table 3). Maternal age and egg mass explained much less variation. Generally, DHA and AA proportions were positively correlated with maternal size, and the EPA proportion was negatively correlated with maternal size in both the neutral and polar lipid fractions (Table 3; Figs. 2, 3). In contrast to the individual trends with AA and EPA, the AA + EPA proportions did not vary with maternal fork length (Fig. 3). The proportion of oleic acid (18:1(n–9)) increased with maternal fork length in the polar but not the neutral lipid fraction (Table 3). The proportion of palmitic acid (16:0) did not vary significantly with maternal size in either egg lipid fraction.

We also examined the relationship between relative abundances of selected fatty acids (those listed in Table 3) and maternal traits using data from all 10 populations and an ANCOVA approach. The model initially included population as a class variable, maternal age, maternal length, and egg size as covariates, and all respective interaction terms. Nonsignificant terms were removed sequentially by backward elimination (partial F test, $P > 0.05$). The population effect was statistically significant in most cases, indicating that the relative abundance of all selected fatty acids differed significantly among populations both in neutral and polar fractions. However, the relationships between these relative abundances and maternal traits were usually not significant. In addition, interactions between population and maternal traits were frequently significant, indicating that the nature of the relationship between relative fatty acid abundances and maternal characteristics varied among populations.

We used the data from the 10 populations to further test for differences in variability of fatty acid profiles between neutral and polar lipid fractions at the intrapopulation (among-female) level. We predicted that among-female variation in fatty acid proportions would be greater in the neutral than in the polar fraction. Coefficients of variation (CVs) for transformed proportions of selected fatty acids were determined (across females) in the neutral and polar fractions for each study population. These CVs for the two fractions were then compared by paired-comparisons t tests using the 10 populations as replicates. Mean CVs were higher in the neutral than the polar fraction for all selected fatty acids, and these differences were statistically significant for AA, DHA, AA + EPA, and the sums of three fatty acid families (Table 4).

Variation among populations

For the interpopulation portion of the study, fish were sampled over a wide geographic area from Arkansas to northern Saskatchewan (Table 1). Walleye growth rates vary greatly over this range (Johnston and Leggett 2002). Our size-selective sampling protocol resulted in low size variation but fairly high age variation among populations (Table 1). As expected, the age of the sampled fish varied significantly among populations (ANOVA, $F = 16.4$, df = 9,49, $P < 0.001$).

Mean egg mass differed significantly among populations (ANOVA, $F = 10.6$, df = 9,49, $P < 0.001$, $R^2 = 0.66$). We reanalyzed the egg mass data by ANCOVA with maternal age and fork length (FL) as covariates to determine if the interpopulation variation in egg mass was due to differences in these maternal traits. Following backwards elimination of nonsignificant terms (partial F test, $P > 0.05$), the final model contained only population and FL × population interaction terms ($R^2 = 0.84$). Replacing the interaction term with maternal age indicated that egg size increased with maternal age across populations but the overall strength of the model was less ($R^2 = 0.70$). Maternal traits can explain some of the egg size variation among populations, but differences persist even after adjustment for these traits.

We next examined variation in egg lipid mass among populations. Lipid mass values for three females from the Primrose Lake population were considered unusually high and were eliminated from these analyses. Among populations, total lipid made up 34.3 ± 2.0% (mean ± one standard deviation) of egg dry mass with 27.1 ± 1.9% and 7.2 ± 0.8% as neutral and polar lipid, respectively (Fig. 4). We first compared egg lipid mass (mg·egg^{-1}) among populations by ANCOVA with maternal age, maternal FL, and egg mass as

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Table 2. Mean percentages (and standard deviations) of total fatty acids for major individual fatty acids,[a] fatty acid families, and fatty acid ratios in neutral and polar lipids of walleye eggs from the 10 populations listed in Table 1.

	Population									
Fatty Acid	Greer's	Ontario	Otter Tail	Superior	Winnibigoshish	Vermilion	Woods	Falcon	Manitoba	Primrose
Neutral lipids										
16:0, palmitic	9.3 (0.5)	10.7 (1.1)	9.7 (0.4)	8.2 (0.4)	8.9 (0.4)	10.7 (1.1)	9.9 (0.8)	9.5 (0.5)	9.2 (0.5)	8.9 (0.3)
16:1(*n*–7), palmitoleic	12.2 (0.4)	19.9 (4.8)	18.2 (2.7)	17.5 (2.6)	16.0 (1.6)	20.1 (1.8)	17.0 (0.9)	14.1 (0.6)	17.8 (0.9)	13.7 (1.3)
18:1(*n*–9), oleic	18.1 (1.5)	20.1 (1.9)	22.2 (1.5)	21.0 (1.0)	18.2 (1.9)	22.9 (2.0)	21.2 (1.0)	19.4 (0.6)	22.3 (1.9)	16.9 (2.1)
18:3(*n*–3), linolenic	6.5 (0.8)	4.6 (1.2)	3.0 (0.3)	4.2 (0.5)	6.3 (0.6)	2.9 (0.7)	6.3 (1.2)	5.9 (0.3)	4.4 (0.6)	4.9 (0.7)
20:4(*n*–6), arachidonic	4.1 (0.4)	1.8 (0.5)	3.1 (0.2)	2.3 (0.2)	2.4 (0.3)	2.6 (0.3)	2.3 (0.2)	2.5 (0.2)	2.2 (0.2)	3.6 (0.3)
20:5(*n*–3), eicosapentaenoic	6.0 (0.6)	5.8 (0.5)	3.2 (0.4)	5.6 (1.3)	4.7 (0.5)	3.3 (0.3)	3.6 (0.7)	3.9 (0.2)	3.5 (0.4)	5.5 (0.7)
22:6(*n*–3), docosahexaenoic	14.9 (0.4)	12.0 (1.7)	11.7 (0.8)	13.7 (1.9)	15.7 (1.8)	12.4 (1.2)	11.5 (0.7)	14.1 (0.7)	14.2 (1.1)	15.7 (2.1)
Sum SFA	14.8 (0.6)	14.9 (1.6)	13.0 (0.6)	12.3 (0.5)	12.3 (0.6)	13.8 (1.2)	13.4 (1.1)	13.3 (0.7)	13.0 (0.5)	12.2 (0.6)
Sum MUFA	38.9 (1.4)	48.9 (4.5)	51.9 (1.8)	46.4 (4.7)	42.9 (3.2)	54.1 (1.8)	49.0 (1.9)	42.7 (1.3)	50.3 (2.4)	40.8 (3.2)
Sum (*n*–6) PUFA	13.4 (0.6)	7.9 (1.7)	12.6 (1.4)	11.1 (1.0)	11.2 (0.8)	10.1 (1.5)	11.4 (0.8)	12.6 (0.6)	10.3 (1.0)	13.8 (1.5)
sum (*n*–3) PUFA	32.9 (1.5)	28.3 (3.3)	22.5 (1.0)	30.2 (4.1)	33.6 (2.8)	22.0 (1.6)	26.2 (2.4)	31.4 (1.2)	26.4 (1.9)	33.1 (3.3)
AA + EPA	10.1 (0.8)	7.6 (0.7)	6.2 (0.4)	7.8 (1.4)	7.0 (0.8)	5.9 (0.4)	5.9 (0.7)	6.3 (0.3)	5.7 (0.6)	9.0 (0.9)
EPA/AA	1.5	3.2	1.0	2.5	2.0	1.3	1.5	1.6	1.6	1.5
DHA/EPA	2.5	2.1	3.7	2.5	3.4	3.8	3.2	3.6	4.1	2.9
Sum (*n*–3) / sum (*n*–6)	2.5	3.6	1.8	2.7	3.0	2.2	2.3	2.5	2.6	2.4
Polar lipids										
16:0, palmitic	19.6 (0.7)	18.1 (0.4)	17.7 (1.0)	18.3 (0.4)	17.6 (1.5)	18.5 (0.5)	17.9 (1.4)	18.1 (0.3)	18.2 (0.8)	18.7 (1.6)
16:1(*n*–7), palmitoleic	1.7 (0.1)	2.3 (0.4)	2.3 (0.4)	2.2 (0.2)	2.3 (0.2)	2.3 (0.2)	2.1 (0.2)	1.7 (0.1)	2.2 (0.1)	1.7 (0.1)
18:1(*n*–9), oleic	6.1 (0.4)	6.9 (0.5)	7.1 (0.3)	7.2 (0.5)	6.9 (0.5)	6.9 (0.4)	6.8 (0.5)	6.1 (0.3)	6.8 (0.2)	6.0 (0.5)
20:4(*n*–6), arachidonic	8.4 (0.4)	6.9 (1.1)	9.9 (0.9)	7.5 (0.7)	7.9 (0.6)	9.2 (0.4)	8.5 (0.4)	8.7 (0.4)	7.6 (0.5)	9.1 (0.7)
20:5(*n*–3), eicosapentaenoic	8.2 (0.3)	11.8 (1.3)	6.0 (0.7)	9.6 (1.2)	8.0 (0.8)	6.3 (0.6)	7.4 (1.3)	7.4 (0.3)	6.6 (0.6)	7.8 (1.1)
22:6(*n*–3), docosahexaenoic	33.1 (1.2)	31.6 (0.8)	33.0 (0.8)	33.5 (0.8)	34.1 (2.1)	35.0 (1.1)	32.8 (1.1)	34.7 (0.7)	35.3 (0.4)	32.8 (1.4)
Sum SFA	28.0 (0.7)	26.0 (0.6)	24.6 (1.0)	25.5 (0.6)	25.8 (2.1)	25.5 (0.6)	26.1 (1.9)	26.0 (0.3)	26.9 (0.8)	26.5 (1.4)
Sum MUFA	13.0 (0.4)	15.9 (0.6)	16.7 (0.6)	15.3 (0.9)	15.8 (0.8)	16.3 (0.6)	15.9 (0.9)	13.9 (0.5)	15.7 (0.6)	14.5 (0.9)
Sum (*n*–6) PUFA	13.7 (0.8)	9.5 (1.5)	14.9 (1.1)	11.5 (0.5)	11.3 (0.6)	13.5 (0.7)	12.6 (0.6)	12.9 (0.8)	11.5 (0.3)	13.1 (0.9)
Sum (*n*–3) PUFA	45.3 (1.4)	48.6 (1.3)	43.8 (0.7)	47.7 (1.4)	47.1 (3.1)	44.7 (0.8)	45.4 (2.4)	47.1 (0.8)	46.0 (0.7)	45.9 (1.7)
AA + EPA	16.6 (0.3)	18.7 (0.6)	15.8 (0.9)	17.1 (0.8)	15.9 (0.7)	15.5 (0.8)	16.0 (1.4)	16.2 (0.3)	14.2 (0.9)	16.9 (1.3)
EPA/AA	1.0	1.7	0.6	1.3	1.0	0.7	0.9	0.8	0.9	0.9
DHA/EPA	4.0	2.7	5.5	3.5	4.3	5.5	4.4	4.7	5.4	4.2
Sum (*n*–3) / sum (*n*–6)	3.3	5.1	2.9	4.1	4.2	3.3	3.6	3.7	4.0	3.5

Note: AA, arachidonic acid; EPA, eicosapentaenoic acid; DHA, docosahexaenoic acid; SFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids.

[a]Other fatty acids routinely found: 12:0, 14:0, 15:0, 16:1(*n*–9), 16:1(*n*–5), 17:0, 17:1(isomer unknown), 18:0, 18:1(*n*–7), 18:2(*n*–6), 18:3(*n*–6), 18:4(*n*–3), 20:0, 20:1(*n*–9), 20:1(*n*–7), 20:2(*n*–6), 20:3(*n*–6), 20:3(*n*–3), 20:4(*n*–3), 22:4(*n*–6), 22:5(*n*–6), and 22:5(*n*–3).

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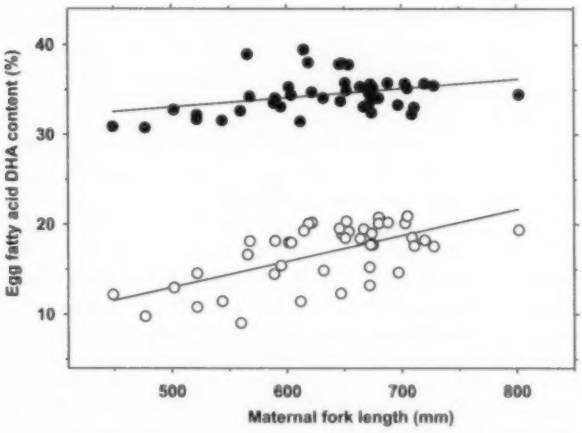
Table 3. Results of regression of proportions for individual fatty acids and of fatty acid ratios in ova against maternal fork length for female walleye of the Lake Ontario population.

Fatty acid	Slope	F	df	R^2	P
Neutral lipids					
16:0	–	1.02	1,41	0.024	0.320
18:1(*n*–9)	+	0.99	1,41	0.024	0.330
20:4(*n*–6), AA	+	23.80	1,41	0.370	<0.001*
20:5(*n*–3), EPA	–	3.65	1,41	0.082	0.063
22:6(*n*–3), DHA	+	27.60	1,41	0.400	<0.001*
DHA/EPA	+	17.80	1,41	0.300	<0.001*
EPA/AA	–	30.20	1,41	0.420	<0.001*
Polar lipids					
16:0	–	2.70	1,41	0.062	0.110
18:1(*n*–9)	+	22.80	1,41	0.36	<0.001*
20:4(*n*–6), AA	+	28.10	1,41	0.41	<0.001*
20:5(*n*–3), EPA	–	24.00	1,41	0.37	<0.001*
22:6(*n*–3), DHA	+	6.17	1,41	0.13	0.017*
DHA/EPA	+	18.60	1,41	0.31	<0.001*
EPA/AA	–	28.80	1,41	0.41	<0.001*

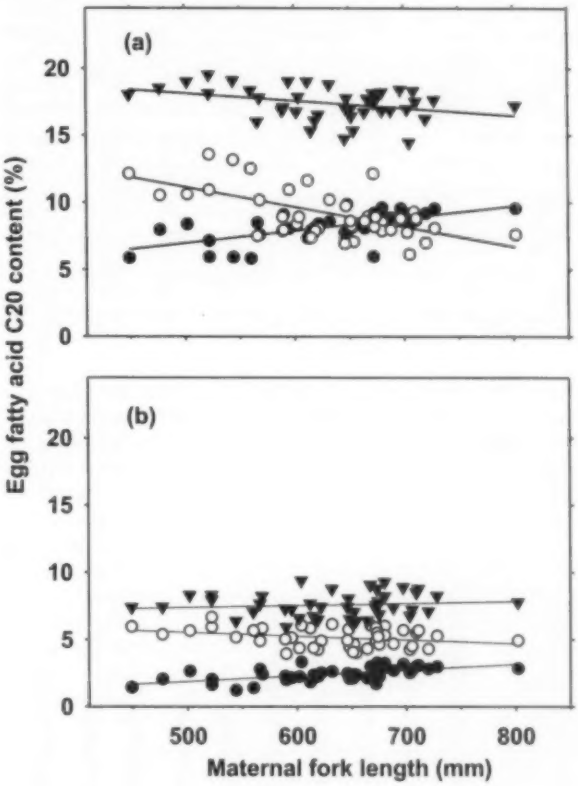
Note: AA, arachidonic acid; EPA, eicosapentaenoic acid; DHA, docosahexaenoic acid. *, statistically significant relationship ($P < 0.05$).

Fig. 2. Percentage of egg fatty acids as docosahexaenoic acid (DHA) in neutral lipids (○) and polar lipids (●) vs. maternal fork length for Lake Ontario walleye (*Sander vitreus*; $n = 42$ females). Lines were fitted by least-squares regression and statistics are summarized in Table 3.



covariates. Following backward elimination of model terms, there was a strong, positive egg mass effect ($F = 46.6$, df = 1,35, $P < 0.001$) and weaker, but significant, stock and stock by age interaction effects ($F > 2.4$, $P < 0.03$). We repeated this analysis using the percentage of egg dry mass as lipid for the dependent variable. All covariate and interaction terms were eliminated from this model, and the remaining stock effect was marginally nonsignificant (ANOVA, $F = 2.01$, df = 9,46, $P = 0.059$, $R^2 = 0.28$). Mean total egg lipid ranged from 31.5% (Otter Tail) to 38.4% (Primrose). Neutral lipid content appeared to be more variable among populations than polar lipid content. The percentage of egg mass as neutral lipid varied significantly among the stocks (ANOVA,

Fig. 3. Percentage of egg fatty acids as arachidonic acid (AA; ●), eicosapentaenoic acid (EPA; ○), and AA + EPA (▼) vs. maternal fork length for Lake Ontario walleye (*Sander vitreus*; $n = 42$ females). Plots are for (*a*) polar and (*b*) neutral lipid fractions. Lines were fitted by least-squares regression, and statistics for AA and EPA are summarized in Table 3. Regressions of AA + EPA vs. fork length were not statistically significant ($P > 0.05$) for either neutral or polar fractions.



$F = 2.45$, df = 9,46, $P = 0.023$), whereas the percentage of egg mass as polar lipid did not (ANOVA, $F = 1.26$, df = 9,46, $P = 0.28$).

Populations differed in the fatty acid profiles of their egg lipids. Percentages of specific fatty acids of interest, totals of the four fatty acid families, and important fatty acid ratios are summarized in Table 2. The first three principal components accounted for 81% of the among-population variation in fatty acid profiles for both the neutral and polar fractions. Scatter plots of the first two principal components indicated that the populations differed more in the fatty acid composition of their neutral lipids than in the composition of their polar lipids (Fig. 5). However, the separation of the populations along these axes was not consistent between the two fractions, and the pattern of separation did not appear to follow any distinct geographical trend.

We predicted that among-population variation in relative abundances of fatty acids would be higher in the neutral than the polar lipid fraction and tested this for several fatty acids (e.g., DHA; Fig. 6) and fatty acid families of particular interest. Comparison of interpopulation CVs indicated that vari-

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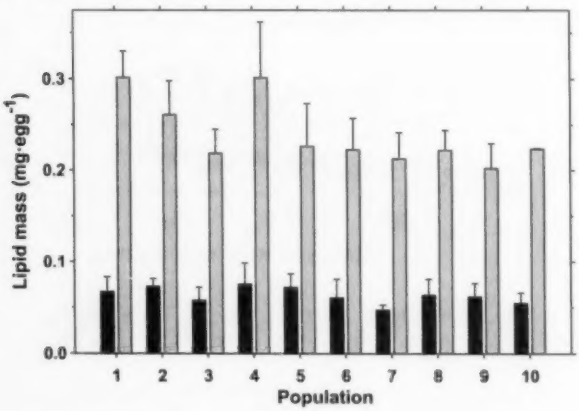
Table 4. Results of paired-comparison *t* tests comparing intrapopulation (among female) coefficients of variation (CV) in fatty acid proportions between neutral and polar lipid fractions of walleye ova for the 10 populations listed in Table 1.

	Mean CV (n = 10)			
Fatty acid	Neutral	Polar	t	P
16:0	3.232	2.606	0.869	0.210
18:1(n–9)	4.212	3.328	1.786	0.060
20:4(n–6), AA	5.488	3.823	2.573	0.015*
20:5(n–3), EPA	6.543	5.459	1.615	0.070
22:6(n–3), DHA	4.786	1.799	4.550	<0.001*
Sum SFA	3.089	2.132	1.613	0.070
Sum MUFA	3.533	2.357	2.627	0.014*
Sum (n–6) PUFA	5.181	3.266	3.365	0.004*
Sum (n–3) PUFA	4.536	1.927	4.603	<0.001*
AA + EPA	5.059	2.671	3.592	0.003*

Note: P values are for one-tailed tests (H_0: neutral CV > polar CV). AA, arachidonic acid; EPA, eicosapentaenoic acid; DHA, docosahexaenoic acid; SFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids. *, statistically significant relationship ($P < 0.05$).

Fig. 4. Masses of neutral (shaded bars) and polar (solid bars) lipids in eggs of walleye (*Sander vitreus*) from 10 North American populations. Population numbers correspond to the listing in Table 1. Values are means + one standard deviation (n = 6 fish per lake; n = 5 fish for population 8, Falcon Lake).

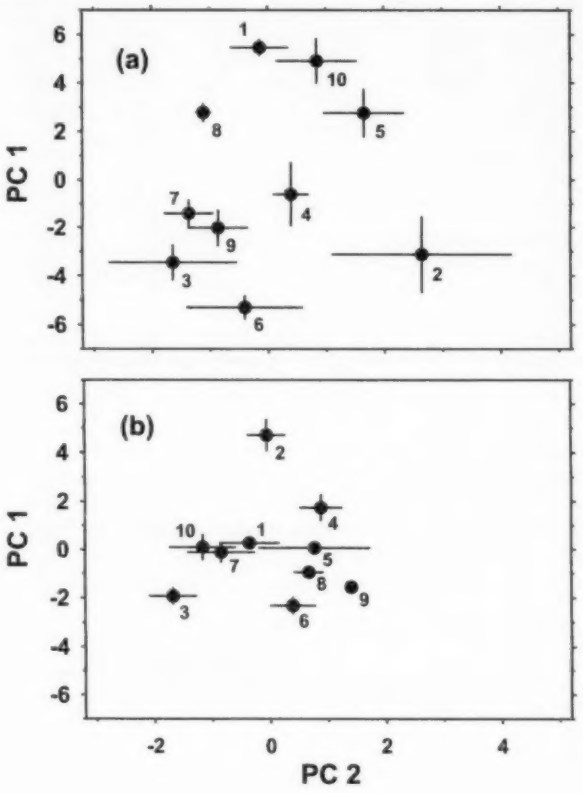


ability was consistently higher in the neutral than in the polar fraction as predicted, and these differences were statistically significant for all but EPA (Fig. 7). Within the polar lipids, variability in DHA was significantly less than that of both EPA and AA ($P < 0.001$) but not significantly different from AA + EPA.

Discussion

Our results indicate that the lipid mass composition of walleye eggs is very consistent both among females and among populations. The total lipid content of walleye eggs increases with egg size but the proportion of egg mass as lipid does not vary with egg size. Similarly, we found that the relative proportions of neutral and polar lipids in walleye eggs did not vary with egg size. Although the proportions of

Fig. 5. Scatter plots of the first two principal components summarized from relative abundances of 29 fatty acids in the (*a*) neutral and (*b*) polar fractions of egg lipids from 10 populations of walleye (*Sander vitreus*). Population numbers correspond to the listing in Table 1. Symbols are population means ± one standard error (n = 6 fish per lake; n = 5 fish for population 8, Falcon Lake).



neutral and polar lipids in fish eggs do change during recrudescence (Wiegand 1996), the mature ova examined in this study had roughly the same lipid class composition over a wide range in mass. Previous research has indicated that total egg mass increases with maternal age and size in some walleye populations (Johnston and Leggett 2002). We therefore predicted that larger or older females might also produce more lipid-rich eggs in some populations. This did not appear to be the case. However, the fatty acid composition of these eggs was related to maternal characteristics.

Fatty acid profiles of the walleye eggs were significantly correlated with maternal size (length) in the Lake Ontario population. In particular, proportions of DHA and AA increased in both lipid fractions, whereas those of EPA declined in the polar lipid fraction. The increase in DHA in the neutral lipid fraction with maternal fork length was particularly steep. Within the polar lipid fraction, AA + EPA was maintained within a narrow range. We did not observe significant relationships between relative proportions of fatty acids and maternal size across walleye populations. However, this may be an artifact of the smaller number and re-

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Fig. 6. Percentage of total fatty acids as docosahexaenoic acid (DHA, 22:6(*n*–3)) in neutral (shaded bars) and polar (solid bars) fractions of egg lipids for walleye (*Sander vitreus*) from 10 North American populations. Population numbers correspond to the listing in Table 1. Values are means + one standard deviation (n = 6 fish per lake; n = 5 fish for population 8, Falcon Lake).

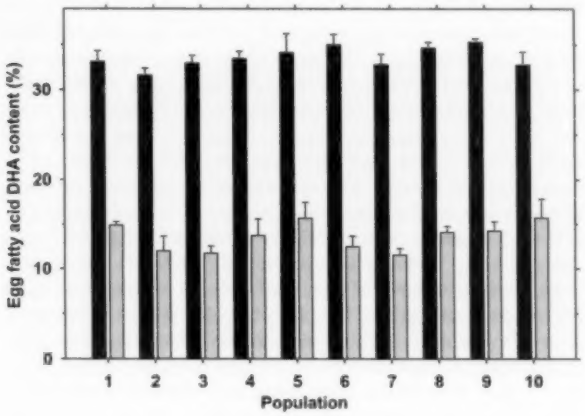
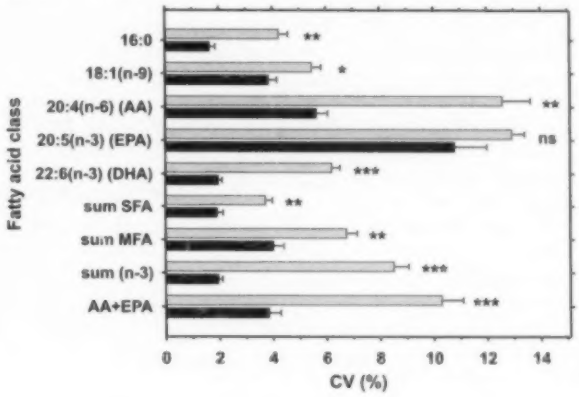


Fig. 7. Comparison of interpopulation variation (CVs) in proportions of selected fatty acid classes and groups between neutral (shaded bars) and polar (solid bars) fractions of egg lipids for walleye (*Sander vitreus*) from 10 North American populations. Values represent jackknifed means + one standard error. Results of two-tailed t tests are indicated (ns, not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).



stricted size range of females sampled for our interpopulation comparison.

The significant relationships between egg fatty acid profiles and maternal traits may be of adaptive significance. Given the multiple essential roles of DHA in the formation and structure of membranes and the potential limitations to its availability in freshwater ecosystems, it is reasonable to hypothesize that by this criterion, larger walleye produce a better, if not a bigger, egg. The mechanism by which the increased DHA in eggs of larger fish originates is unknown; several possibilities exist. Larger females may have larger reserves of DHA to draw upon during vitellogenesis than smaller females. This may arise if the diet of larger females is richer in DHA or if larger females can selectively catabolize MUFA (and SFA) and retain DHA and other PUFA. This latter phenomenon has been reported in other species during embryonic and larval development (Rønnestad et al. 1995; Wiegand 1996; Mourente et al. 1999). Selective mobilization of DHA in support of vitellogenesis has also been observed in several species (Wiegand 1996), consistent with the essential nature of this fatty acid in ova. Larger females may be more willing (in the evolutionary sense) to devote a larger proportion of their somatic DHA reserves to reproduction at the expense of somatic requirements than smaller females, particularly towards the end of their reproductive lives as the probability of future spawning declines.

The situation with respect to the C20 EFA is less clear. Both AA and EPA play a structural role in membrane systems, EPA being the more prominent in fish, especially in marine species (Bell and Dick 1991; Sargent et al. 1999*b*). In addition, AA and EPA compete for enzymes in cyclooxygenase and lipoxygenase pathways linked to the synthesis of eicosanoids (Tocher et al. 1991; Knight et al. 1995; Bell et al. 1996), with AA generally being the preferred substrate (Tocher et al. 1996). Either phosphatidyl choline or phosphatidyl inositol can be the source of C20 eicosanoid precursor (Tocher et al. 1991). This dual source complicates interpretation of fatty acid compositional data, even when individual glycerophospholipids have been isolated and analysed. High content of EPA in broodstock diets and in eggs has been linked to reduced production of viable larvae (Fernandez-Palacios et al. 1995), whereas stress-related pathologies in young fish have been associated with low levels of EPA relative to AA (EPA:AA) (Sargent et al. 1995). Optimum dietary and tissue EPA:AA differ among species, and the best indicators are likely to be derived from studies of wild populations (Sargent et al. 1999*b*).

In walleye, a significant negative correlation has been observed between survival and EPA:AA in whole-body phospholipids of 3-week-old juveniles (Czesny et al. 1999). In the present study, the EPA:AA in both egg lipid fractions declined with maternal length in the Lake Ontario walleye population (Fig. 8). One possible interpretation is that the decrease in EPA:AA with maternal size represents an adaptive response by larger fish to produce a better egg. Alternatively, as with other fatty acids, the results may simply reflect dietary differences among different-sized females and be of no adaptive significance. The optimum EPA–AA ratios for walleye in the NL and PL fractions of their eggs remain to be determined.

This is the first study to report egg fatty acid compositional data for a freshwater fish species from such a large number of populations over a wide geographic range. Our data indicate that relative abundances of the fatty acids differ significantly among populations. The adaptive significance of this variation, if any, is unknown. The observed pattern in variation did not follow any discernible geographic pattern. Walleye egg size varies among populations with respect to both latitude and water body productivity (Johnston and Leggett 2002). It is not unreasonable to predict that walleye populations at higher latitudes should produce eggs with higher proportions of PUFA and lower proportions of SFA because of the higher requirements for PUFA in membrane assembly under cooler conditions. Such a latitudinal trend

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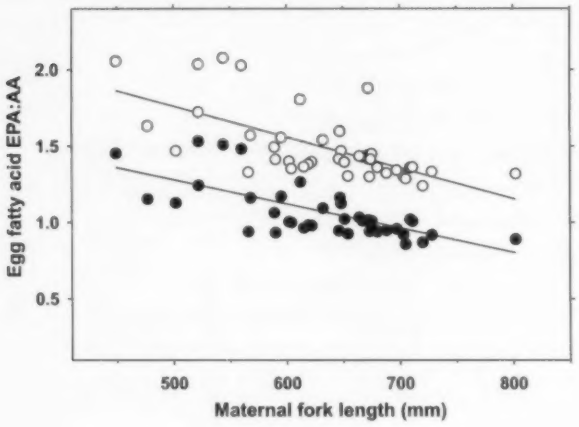
Fig. 8. Ratio of relative abundance of 20:5(*n*–3) to 20:4(*n*–6) (EPA/AA) in neutral (○) and polar (●) egg lipids vs. maternal fork length for Lake Ontario walleye (*Sander vitreus*; $n = 42$ females). Lines were fitted by least-squares regression and are statistically significant ($P < 0.001$, $R^2 > 0.40$).



was not evident in our data. Given that walleye spawn within a narrow temperature range at all latitudes, such an adaptation may not be required. Embryos and larvae of some species increase their retention of DHA when developing at cooler temperatures (Wiegand et al. 1991), but it is unknown if walleye are capable of this.

We found a higher level of consistency in the fatty acid profiles in the polar lipid fraction than in the neutral lipid fraction of walleye eggs. This was evident in comparisons among females within populations but was more pronounced in comparisons among populations. It was particularly noteworthy that levels of DHA and the total C20 EFA (AA + EPA) were significantly less variable in the polar than in the neutral lipids both among females and among populations. The fatty acid composition of polar lipid may be less variable because of its origin.

Egg polar lipid derives from the plasma lipoprotein yolk precursor, vitellogenin (Vtg), whereas neutral lipid is likely accumulated primarily from plasma very low density lipoprotein (VLDL) and from Vtg and endogenous synthesis within the oocyte (Wiegand 1996). The accumulation of Vtg by oocytes has been studied in detail at the quantitative, time course, and mechanistic levels (Tyler and Sumpter 1996), and a detailed model has been presented for its structure and incorporation of phospholipids (Anderson et al. 1998; Carraway et al. 2000; Thompson and Banaszak 2002). In this model, vitellogenin and related lipoproteins accumulate lipid in a conical cavity during translation. According to the model, the phospholipid is derived from intracellular membrane leaflets. Vitellogenin fatty acid complement would then be determined by the membrane composition and possibly limited by steric conditions within the protein cavity. The metabolism of VLDL, especially as it relates to ovarian recrudescence, has received much less attention (Black and Skinner 1987; Wallaert and Babin 1992, 1994) despite its obvious significance (Silversand et al. 1996; Ungerer and Thomas 1996). In fish, plasma VLDL is of both hepatic and intestinal origin (Babin and Vernier 1989). This lipoprotein class contains a central core of triacylglycerol, which is assembled separately from the surface apoprotein (Carraway et al. 2000; Shelness and Sellers 2001). VLDL fatty acids are derived from lipid depots, hepatic synthesis, and the diet. The different mechanism of assembly suggests that fatty acid composition of VLDL would be much more variable than that of Vtg.

Another question that we addressed was variability of EFA within the polar lipid fraction. In the polar lipids, we observed a high consistency in proportions of AA + EPA compared with proportions of either fatty acid individually. Also, AA + EPA was significantly less variable in the polar lipid fraction than in the neutral lipids. We find this observation interesting because of the potential for competition between AA and EPA as precursors in eicosanoid synthesis pathways and the observed relationship between the EPA–AA ratio and offspring viability (Czesny et al. 1999). It suggests a high level of control of the total amount of essential C20 PUFA incorporated into the phospholipid layers accumulated by vitellogenin during its formation, with less specificity as to amounts of the individual C20 fatty acid. Preferential incorporation of specific fatty acids into individual phospholipid classes has been observed in fish cell lines (Tocher 1990; Tocher and Dick 1990). However, to our knowledge, this has not been studied in fish liver engaged in Vtg production.

Within egg polar lipids, a higher degree of regulation of egg polar lipid DHA than EPA has been observed in studies involving manipulation of broodstock diets (Wiegand 1996; Almansa et al. 1999; Bruce et al. 1999). A similar observation has been made in the comparison of wild and domesticated populations of walleye (Czesny and Dabrowski 1998) and sturgeon (*Acipenser* spp.) (Czesny et al. 2000).

The opposite situation has been found in cod. In a study of two cod populations, DHA levels were higher and AA levels were lower in eggs of the generally inferior Baltic population than in eggs of the Skagerrak population (Pickova et al. 1997). The observed difference between the two populations was attributed to different selection pressures. In contrast, EPA levels were similar in the polar lipids of eggs from both populations. Polar lipids in the eggs of Baltic cod held in captivity from 2 to 24 months differed very little in composition (Pickova et al. 1997). This suggests that egg polar lipid fatty acid profiles are tightly regulated in cod.

In contrast to cod, we observed lower interpopulation variability in DHA than EPA in egg lipids of walleye, perhaps because DHA is more limiting in freshwater than in marine ecosystems. In many freshwater invertebrates, EPA is the more abundant highly unsaturated (*n*–3) fatty acid, whereas the availability of DHA in these species may be problematic. Freshwater copepods contain significant quantities of DHA (Desvilettes et al. 1994), but DHA levels are lower in other potential prey items such as cladocerans and insects (Bell et al. 1994; Desvilettes et al. 1994; Ghioni et al. 1996). Copepods are commonly consumed by first-feeding walleye larvae, but their contribution to the diet typically declines sharply as walleye grow (Fox 1989; Johnston and Mathias 1994). There may be a selective advantage to incorporating high levels of DHA into egg lipids where the prey available to offspring is low in DHA.

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Besides diet, the other potential source of highly unsaturated fatty acids is synthesis from C18 precursors, namely 18:2(*n*–6) and 18:3(*n*–3). The C18 PUFA can satisfy the EFA requirements of some freshwater fish, indicating that they can produce AA, EPA, and DHA by elongating and desaturating the C18 precursors (Sargent et al. 1995). However, mature pike (*Esox lucius* L.), another freshwater piscivore, appear to have low activity of the desaturase enzyme necessary for formation of AA, EPA, and DHA (Henderson et al. 1995; Buzzi et al. 1997). The capacity of walleye to synthesize HUFA from C18 precursors remains to be determined.

In an earlier study on eggs pooled from 109 Lake Manitoba walleyes and then sorted on the basis of size, complete mortality occurred by 11 days posthatch in larvae from the smallest eggs (Moodie et al. 1989). The smallest eggs also had the lowest DHA percentage in the LPY + blastoderm fraction (isolated by centrifugation 72 h after fertilization). Low DHA can clearly occur in wild freshwater fish eggs and may be associated with low egg quality. Although the study of Moodie et al. (1989) and the current study are not strictly comparable because of important methodological differences, they are consistent concerning the importance of egg DHA in wild walleye eggs. The work of Moodie et al. (1989) suggests consequences of low DHA in early development, whereas the present study shows the extent of variation in egg DHA content.

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A simulation study of impacts of error structure on modeling stock–recruitment data using generalized linear models

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Abstract: Stock–recruitment (*S–R*) models are commonly fitted to *S–R* data with a least-squares method. Errors in modeling are usually assumed to be normal or lognormal, regardless of whether such an assumption is realistic. A Monte Carlo simulation approach was used to evaluate the impact of the assumption of error structure on *S–R* modeling. The generalized linear model, which can readily deal with different error structures, was used in estimating parameters. This study suggests that the quality of *S–R* parameter estimation, measured by estimation errors, can be influenced by the realism of error structure assumed in an estimation, the number of *S–R* data points, and the number of outliers in modeling. A small number of *S–R* data points and the presence of outliers in *S–R* data could increase the difficulty in identifying an appropriate error structure in modeling, which might lead to large biases in the *S–R* parameter estimation. This study shows that generalized linear model methods can help identify an appropriate error distribution in *S–R* modeling, leading to an improved estimation of parameters even when there are outliers and the number of *S–R* data points is small. We recommend the generalized linear model be used for quantifying stock–recruitment relationships.

Résumé : On a l'habitude d'ajuster les modèles stock–recrutement (*S–R*) aux données *S–R* à l'aide d'une méthode des moindres carrés. On présuppose que les erreurs de modélisation suivent une distribution normale ou lognormale, sans tenir compte si cette présupposition est réaliste ou non. Une simulation de type Monte Carlo nous a permis d'évaluer l'impact de la présupposition d'une structure d'erreur sur la modélisation *S–R*. Le modèle linéaire généralisé, qui peut s'accommoder facilement de diverses structures d'erreur, a servi à estimer les paramètres. Notre étude laisse croire que la qualité de l'estimation des paramètres *S–R*, reflétée dans les erreurs d'estimation, peut être influencée par le réalisme de la structure d'erreur choisie pour l'estimation, par le nombre de données de *S–R* et le nombre de données aberrantes dans la modélisation. Un petit nombre de données *S–R* et la présence de données aberrantes dans les données *S–R* peuvent rendre plus difficile l'identification d'une structure d'erreur appropriée dans la modélisation, ce qui peut mener à de fortes distorsions dans l'estimation des paramètres *S–R*. Notre étude démontre que les méthodes reliées au modèle linéaire généralisé permettent de définir une distribution d'erreur appropriée dans la modélisation *S–R*, ce qui mène à une meilleure estimation des paramètres, même lorsqu'il y a des données aberrantes et qu'il y a peu de données *S–R*. Nous recommandons l'utilisation du modèle linéaire généralisé pour quantifier les relations stock–recrutement.

[Traduit par la Rédaction]

Introduction

Stock–recruitment (*S–R*) models are mathematical functions that describe relationships between spawning stock abundance and subsequent recruitment. Future recruitment, which is essential for fisheries management, can be estimated from current spawners using *S–R* models (Hilborn and Walters 1992).

Large variations in recruitment have been observed for many fish species (e.g., Myers and Barrowman 1996; Power 1996; Hinrichsen 2001). The variations tend to increase with spawning stock biomass (Myers et al. 1995), which has led to wide adoption of the assumption that recruitment at a given level of spawning biomass follows a lognormal distribution (Hilborn and Walters 1992). This has been used as an alternative to the normal distribution (Hennemuth et al. 1980; Quinn and Deriso 1999; Hinrichsen 2001). The normal error distribution assumption is no longer widely used in *S–R* analyses, although it tends to be more realistic if the survival of individuals during their early life stages is density-independent and constant (Shelton 1992).

Error structure is an integral part of modeling (Carroll and Ruppert 1984; Schnute 1991; Chen and Paloheimo 1998). The impact of unrealistic assumptions of model error struc-

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ture on parameter estimation has been evaluated with various fisheries models (Deriso et al. 1985; Bajdik and Schneider 1991; Cadigan and Myers 2001). Inappropriate error distribution assumptions can cause inaccurate estimates of model parameters, their variability, and the attained significance level of the fitted model. In this study, using a Monte Carlo simulation approach, we evaluated the importance of having a proper error distribution assumption and the effectiveness of using a generalized linear model in identifying a proper error distribution in modeling *S–R* data.

The generalized linear model (GzLM) is a maximum likelihood based method that provides a systematic framework by which parameters are estimated when the model error structure belongs to the exponential family. We considered several error structures in the exponential family, including normal, lognormal, gamma, and Poisson distributions. The likelihood of recruitment having normal or lognormal distributions was discussed in Shelton (1992) and Fogarty (1993). Lognormal and gamma distributions were used by Myers et al. (1995). The Poisson distribution is considered appropriate for counting data and for nonnegative and highly varied data (Bajdik and Schneider 1991; White and Bennetts 1996) and may be appropriate for recruitment.

Because the number of *S–R* data is often small (Hilborn and Walters 1992) and outliers are likely to be present in the *S–R* data (Chen and Paloheimo 1995; Hinrichsen 2001), the role of sample size and outliers in identifying appropriate error structure in *S–R* modeling was also evaluated in the simulation study.

The theory of GzLM was developed in the 1970s (Nelder and Wedderburn 1972) and later was expanded in theory and application during the 1980s and 1990s (McCullagh and Nelder 1983, 1989; Dobson 1990). The GzLM can be implemented by various software such as GLIM (Numerical Algorithms Group Ltd., Oxford, U.K.), SAS (SAS Institute Inc., Cary, N.C.), and SPLUS (MathSoft Engineering and Education Inc., Cambridge, Mass.). MATLAB (Math Works Inc., Natick, Mass.) was used in this study.

Materials and methods

Data simulation

We used the Cushing (eq. 1), Ricker (eq. 2), and Beverton–Holt (eq. 3) models (Quinn and Deriso 1999) as examples in modeling *S–R* data:

$$(1) \qquad R = \alpha S^{\beta}$$

$$(2) \qquad R = \alpha S e^{-\beta S}$$

$$(3) \qquad R = \alpha S/(1 + \beta S)$$

where α and β are two parameters to be estimated, and S and R are the spawning stock biomass and its subsequent recruitment, respectively. The Ricker and Beverton–Holt models consider a density-dependent effect, but the Cushing model does not. In practice, the choice of these models depends on the data. In this study, we considered the Cushing model first. Two scenarios were used in simulating *S–R* data with eq. 1. One scenario was to randomly sample S data from 1000 to 10 000 values using a uniform distribution and then calculate corresponding R values according to eq. 1 and an assumed error structure, which includes normal, lognormal, gamma, and Poisson functions (Table 1). The values of 2.012 and 0.857 were used for $\ln(\alpha)$ and β, respectively, in simulating the R data from the S data, which were taken from the pink salmon (*Oncorhynchus gorbuscha*) fishery in northern southeast Alaska (Quinn and Deriso 1999). For the second scenario, the *S–R* data were simulated using actual S data of pink salmon in northern southeast Alaska using the four types of error distributions listed in Table 1 and the two parameters for the pink salmon described above. The data simulated in the first and second scenarios are referred to as the first and second data sets, respectively, in this paper.

We then repeated the above approach for the Ricker and Beverton–Holt models (i.e., eqs. 2 and 3). The values used for the two parameters were $\ln(\alpha) = 1.047$ and $\beta = 5.52 \times 10^{-5}$ in the Ricker model and $\ln(\alpha) = 1.042$ and $\beta = 5.92 \times 10^{-5}$ in the Beverton–Holt model, also taken from the pink salmon stock.

Generalized linear model (GzLM)

The generalized linear model is sometimes abbreviated as GLM (McCullagh and Nelder 1989; Lindsey 1997; Myers et al. 2001), GLIM (software distributed by Numerical Algorithms Group), or GLZ (StatSoft Inc., Tulsa, Okla.). In this paper, we use GzLM to differentiate the generalized linear model from the general linear model (GLM) and the software GLIM.

A GzLM has three components (McCullagh and Nelder 1989). One is the random component $\mathbf{Y}$, which is a vector of observations y having n components that are independently distributed with means $\boldsymbol{\mu}$. The second is the systematic component, which is a specification for the vector $\boldsymbol{\mu}$ in terms of a small number of unknown parameters $\beta_1, \beta_2, \ldots, \beta_p$. A linear predictor $\boldsymbol{\eta}$ is given by $\boldsymbol{\eta} = \sum_{j=1}^{p} \mathbf{X}_j \beta_j$, where $\mathbf{X}$ is the model matrix or the covariates for observation $\mathbf{Y}$. The third component is the link between the random and systematic components. It is often written as $\boldsymbol{\eta} = g(\boldsymbol{\mu})$, where g is the link function (McCullagh and Nelder 1989). In the case of the GLM, $\boldsymbol{\eta} = \boldsymbol{\mu}$ (i.e., identity link). Thus GLM is a special case of GzLM. The likelihood function of $\mathbf{Y}$ can be written as

$$(4) \qquad L = \prod_{1}^{n} f(y;\theta)$$

where f is the probability distribution function (pdf) which depends on the parameter(s) θ. If the pdf is a member of the exponential class, when $\mathbf{Y}$ is a discrete type, then we could have

$$(5) \qquad f(y;\theta) = \exp[p(\theta)K(y) + s(y) + q(\theta)], \quad y = a_1, a_2, a_3, \ldots$$
$$= 0, \quad \text{elsewhere}$$

The log-likelihood function is then

$$(6) \qquad \mathrm{LL} = p(\theta)\sum_{1}^{n} K(y_i) + \sum_{1}^{n} S(y_i) + nq(\theta)$$

and where $\sum_{1}^{n} K(y_i)$ is a sufficient statistic for the parameter θ and $p(\theta)$ is the canonical link for a distribution for which the pdf is $f(y;\theta)$. Here, $\mathbf{Y}$ is recruitment R, $\mathbf{X}$ is spawning

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Table 1. The distributions, their corresponding canonical links, and links used in this paper.

Distribution	Canonical link	Links used in this paper	
		Cushing and Ricker models	Beverton–Holt model
Normal	$\eta = \mu$	$\eta = \log(\mu)$	$\eta = 1/\mu$
Lognormal (log-transformed data)	$\eta = \mu$	$\eta = \mu$	
Gamma	$\eta = 1/\mu$	$\eta = \log(\mu)$	$\eta = 1/\mu$
Poisson	$\eta = \log(\mu)$	$\eta = \log(\mu)$	$\eta = 1/\mu$

stock biomass S, and θ represents the parameters in the S–R models.

The exponential family includes the normal, Poisson, gamma, and other distributions. The link function $\eta = g(\mu)$ relates the mean of the response variable $\boldsymbol{Y}$ to the linear combination of the $\mathbf{X}_i$. Common choices of link functions include identity, logarithmic, reciprocal, power, and logit (McCullagh and Nelder 1989; The Math Works Inc. 2002). The GzLM is flexible to incorporate different links and not be limited to the canonical links. The links that we used in this paper were based on the S–R model structure, because we did not consider changing the S–R model form. The choice of the link functions did not affect the assumption about the distribution of $\boldsymbol{Y}$ in GzLM. The distributions, their corresponding canonical links, and links used in this paper are shown in Table 1. The GzLM model was used to estimate the parameters given the link function $\eta = g(\mu)$ according to the maximum log-likelihood method (i.e., eq. 6). The parameters were then used to calculate the expected value of the response variable (i.e., recruitment) and then the residuals. Homogeneity of residuals was evaluated and used as a criterion to determine if the model error structure was appropriate. When different model error assumptions were used in a GzLM, the one that resulted in homogeneous residuals was considered as the most appropriate one (McCullagh and Nelder 1989). An example resulting from the application of GzLM with the four error distributions to S–R data simulated with a normal distributed error is shown (Fig. 1). This example suggests that residuals tend to be homogeneous when error distribution is correctly defined in the GzLM.

The GzLM parameter estimations for stock–recruitment models

Cushing model

A log transformation in conjunction with a normal error assumption is commonly used in fitting the Cushing model to S–R data. This is equivalent to assuming that the untransformed recruitment has a lognormal distribution. With the lognormal transformation, the Cushing model (i.e., eq. 1) can be rewritten as

$$\ln(R) = \ln(\alpha) + \beta \ln(S) + \varepsilon \tag{7}$$

where ε has a normal distribution defined as $N(0,\sigma^2)$; $\ln(R)$ is the dependent variable and $\ln(S)$ is the independent variable in the GzLM. The identity link $\eta = \mu$ is used, and the choice of error is normal. The parameter estimates are the same as those from the GLM model after the Cushing model is log transformed (i.e., eq. 7).

For error distributions that are normal, gamma, and Poisson, we can rewrite the Cushing model as

$$E(R) = \alpha S^{\beta} = e^{\ln(\alpha)+\beta\ln(S)} \tag{8}$$

Model parameters are estimated based on the assumption of the distribution of R. In the GzLM analysis, R is the dependent variable and $\ln(S)$ is the independent variable. The log link is used, and the error choice is normal, gamma, and Poisson, respectively. The parameter estimates using a normal error distribution are the same as those estimated using a nonlinear least-squares method.

Ricker model

When the lognormal distribution is assumed for the error distribution of the Ricker model, eq. 2 can be rewritten as

$$\ln(R) = \ln(\alpha) - \beta S + \ln(S) + \varepsilon \tag{9}$$

which is equivalent to

$$R = S e^{\ln(\alpha)-\beta S} e^{\varepsilon} \tag{10}$$

where ε follows $N(0,\sigma^2)$; $\ln(R)$ is the dependent variable, negative S is the independent variable, and $\ln(S)$ is an offset in the GzLM. The identity link $\eta = \mu$ is used, and the choice of error is normal. The parameter estimates are the same as those from the GLM model after linearizing the Ricker model. The commonly used linearization method, which can be expressed as

$$R/S = e^{\alpha-\beta S} + \varepsilon \tag{11}$$

is likely to introduce estimation errors because variable S appears in both sides of the equation (Quinn and Deriso 1999).

For error distributions that are normal, gamma, and Poisson, the Ricker model can be written as

$$E(R) = e^{\ln(\alpha)-\beta S+\ln(S)} \tag{12}$$

Model parameters are estimated based on the assumption of the distribution of R. R is the dependent variable, negative S is the independent variable, and $\ln(S)$ is an offset in the GzLM. The log link $\eta = \log(\mu)$ is used, and the choice of error is normal, gamma, and Poisson, respectively.

Beverton–Holt model

When the normal, gamma, or Poisson distribution is assumed for the error distribution of the Beverton–Holt model, eq. 3 can be rewritten as

$$E(R) = \frac{1}{\frac{1}{\alpha S} + \frac{\beta}{\alpha}} \tag{13}$$

Model parameters are estimated based on the assumption of the distribution of R. R is the dependent variable and $1/S$ is the independent variable in the GzLM. The reciprocal link

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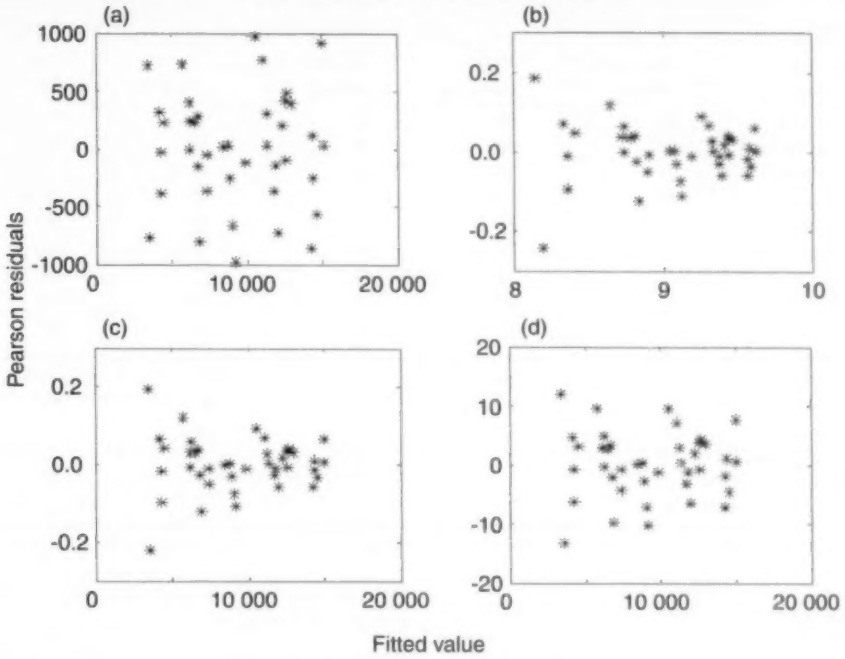
Fig. 1. An example for showing the homogeneity and heterogeneity of residual distributions. Pearson residuals were used. The model error distribution used in simulating the stock–recruitment data is normal; the model error distributions used in the generalized linear model for the parameter estimation are (*a*) normal, (*b*) lognormal, (*c*) gamma, and (*d*) Poisson.



$\eta = 1/\mu$ is used, and the choice of error is normal, gamma, and Poisson, respectively.

For error distributions that are lognormal, the Beverton–Holt model can be written as

$$(14)\quad \ln(R) = \ln\frac{\alpha S}{1+\beta S} + \varepsilon$$

$$= \ln(\alpha) + \ln(S) - \ln(1+\beta S) + \varepsilon$$

where ε is the error term following $N(0,\sigma^2)$. Because of the nonlinear parameters in the above equation, the code and method used to get the parameter estimate are complicated and approximated when using GzLM. Equation 14 can be regarded as a nonlinear equation with a normally distributed error structure, where $\ln(R)$ is the response variable and S is the independent variable. Considering the fact that the parameter estimate using GzLM in eq. 14 equals that using the nonlinear least-squares estimate, a nonlinear least-squares method was used in solving this equation instead of GzLM.

Simulation design

The following procedure was used in the simulation: (*i*) simulate *S–R* data sets using the Cushing model for error scenarios (listed in Table 2) with the total number of observations being 10, 20, and 40; and (*ii*) simulate *S–R* data sets with outliers by adding atypical errors to 10%, 20%, and 40% of the data, with the number of observations being 40. Both of the *S–R* data sets discussed previously in the Data simulation section were used in simulating data with and without outliers. The same approach was then applied to the Ricker model. The combination of three models (Cushing, Ricker, and Beverton–Holt), two data sets (randomly drawn *S* data and true *S* data for the pink salmon), four error distributions used in simulating the *S–R* data (normal, lognormal, gamma, and Poisson), four error distributions assumed in the GzLM for parameter estimation (normal, lognormal, gamma, and Poisson), three sample sizes (10, 20, and 40 *S–R* observations), and three different levels of outlier contaminations (10%, 20%, and 40%) at the sample size of 40 resulted in 480 simulation scenarios in total evaluated in this study. When adding outliers in the simulation study, if 10% of outliers were added, 90% of *S–R* data with the supposed model error structure were first simulated and then another 10% of the outliers with another model error structure were simulated. Finally, the 90% common data and 10% outliers were added together before the generalized linear model was used to estimate the parameters. For each simulation scenario, 1000 simulations were run to derive the stable results.

Departure of the estimated parameters from the true values was measured by the relative estimation bias (REB; eq. 15), relative estimate error (REE; eq. 16), and root mean square error (RMSE; eq. 17):

$$(15)\quad \mathrm{REB}(\%) = \frac{\left(\sum_1^N \beta_i^*\right)\Big/N - \beta}{\beta} \times 100$$

$$(16)\quad \mathrm{REE}(\%) = \frac{\sum_1^N \left|\beta_i^* - \beta\right|}{N\beta} \times 100$$

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Table 2. Comparison of the regression method proposed in this paper with the commonly used visual checking method in identifying the residual homogeneity for the 100 simulations (in this study, the Cushing model was used).

Model error distribution		Simulations with homogeneous residuals (%)					
		Sample size = 10		Sample size = 20		Sample size = 40	
in simulating *S–R* data	in GzLM estimation	Regression method	Visual checking	Regression method	Visual checking	Regression method	Visual checking
Normal	Normal	87	88	93	88	92	87
	Lognormal	70	68	40	48	10	16
	Gamma	72	70	43	47	10	13
	Poisson	83	77	80	80	40	40
Lognormal	Normal	82	57	65	40	20	18
	Lognormal	97	75	85	75	82	87
	Gamma	88	72	82	77	85	93
	Poisson	87	63	75	58	57	50
Gamma	Normal	82	47	57	43	33	27
	Lognormal	80	72	87	77	70	70
	Gamma	83	78	87	83	70	70
	Poisson	83	60	78	62	73	58
Poisson	Normal	83	62	70	62	43	40
	Lognormal	87	60	72	52	53	58
	Gamma	85	63	75	47	53	58
	Poisson	88	67	80	77	93	87

Note: The results derived for different sample sizes (10, 20, and 40) are compared. GzLM, generalized linear model; *S–R*, stock–recruitment.

$$\text{(17)}\quad \text{RMSE} = \left(\frac{\sum_{1}^{N} (\beta_i^* - \beta)^2}{N} \right)^{1/2}$$

where β_i^* is the estimated parameter value in the ith simulation, N is the number of simulations, and β is the true parameter value. The smaller the REB, REE, and RMSE values, the better the estimation approach performs.

Quantification of residual's homogeneity

Pearson residuals of the model fitting were calculated for each simulation scenario. Pearson residuals are the differences between observed and predicted values, standardized (divide by the estimated standard deviation of the fitted value) to make their variance (theoretically) constant. If the error distribution assumed in the estimation was consistent with the error distribution used in simulating the *S–R* data, then a plot of resultant Pearson residuals should show constant variances. Thus, to determine if the residuals are homogeneous, one can look at the residual diagnostic plot. A visual inspection of residual diagnostic plots is commonly used in evaluating the residual homogeneity, although the approach may be subjective, particularly when sample sizes are small. In this study, because 1000 simulations were run for each scenario to derive stable results, direct observation was laborious. Thus, we used the following quantitative method to evaluate the homogeneity of the residuals. (*i*) Regress the Pearson residual value (r) and the model predicted value ($\hat{R}$), i.e.,

$$\text{(18)}\quad r = a_1 + b_1\hat{R}$$

Estimate the p value for b_1 to determine if it was significantly different from zero; $\alpha = 10\%$ was used. (*ii*) Regress the absolute Pearson residual value (r_2) and the model predicted value ($\hat{R}$), i.e.,

$$\text{(19)}\quad r_2 = a_2 + b_2\hat{R}$$

Estimate the p value for b_2 to determine if it was significantly different from zero; $\alpha = 10\%$ was used. (*iii*) If both of the estimated p values were larger than $\alpha = 10\%$, we regarded the residuals as homogeneous, otherwise we regarded the residuals as not homogeneous. Many of the residuals show a right or left triangular-shaped pattern symmetric about the x axis when an inappropriate model error structure was used; therefore, we double-checked this situation by using both residuals and absolute value of residuals in the regression. This proposed method, referred hereafter as the regression method, was compared with the commonly used method, which involves visual examination of residual homogeneity, in 100 simulations to determine if both methods derived consistent conclusions in evaluating the residual homogeneity.

Results

The efficiency of the regression method in identifying the residual homogeneity was influenced by sample size (Table 2). When the sample size was 10, the percentage of the simulations with homogeneous residuals was 81% on average. This increased slightly with an increase in sample size (averaged 84% and 89% for sample sizes of 20 and 40, respectively; Table 2). A comparison of the regression method with the commonly used visual-checking method for the residual homogeneity suggests that the proposed regression method effectively identified the simulations that had homogeneous residuals.

When the error distributions used in the GzLM analysis were the same as those used in simulating *S–R* data, percent-

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Table 3. Summary of the simulations in which the model error distributions used in the generalized linear model analyses were the same as those used in simulating stock–recruitment (*S–R*) data.

Model error distribution in simulating *S–R* data	No. of observations	Simulations with homogeneous residuals (%)	REB for ln(α) (%)	REB for β (%)	RMSE for ln(α)	RMSE for β
Normal	10	71.9	0.15	0.04	0.4398	0.0518
	20	79.1	0.02	0.01	0.2989	0.0351
	40	80.4	0.02	0.05	0.2106	0.0248
Lognormal	10	74.3	6.90	1.93	2.9511	0.3585
	20	79.4	0.01	0.19	1.9812	0.2413
	40	80.8	2.21	0.60	1.3260	0.1618
Gamma	10	71.3	0.61	0.15	0.4516	0.0542
	20	73.5	0.73	0.21	0.2915	0.0351
	40	79.1	0.37	0.10	0.1860	0.0224
Poisson	10	73.6	0.026	0.008	0.0724	0.0086
	20	78.5	0.026	0.008	0.0491	0.0059
	40	80.6	0.008	0.002	0.0342	0.0041

Note: The Cushing model and the first set of data, which had *S* values randomly drawn from 1000 to 10 000 values, were used in the simulation. Relative estimate bias (REB) and root mean square error (RMSE) for parameters are shown.

ages of the simulations that had homogeneous residuals increased with an increase in sample size (Table 3). The REEs and RMSEs for α and β tended to decrease with increasing sample size (Fig. 2; Table 3). The REBs of α and β for the sample size of 40 tended to be larger than those for the sample size of 20, but still smaller than for the sample size of 10. Because the REB is the difference between the mean parameter estimate in total simulation runs and the true value divided by the true value, the variance among the simulation runs was hidden. The REB estimate is unsteady compared with the REE and RMSE estimates, which accumulate error in every simulation run. (We did not show the REE estimates in the tables; we only show it in Fig. 2 as an example.)

When the error distributions used in the GzLM analysis differed from those used in simulating *S–R* data, percentages of the simulations with homogeneous residuals became smaller with an increase in sample size (Table 4). This was different from the observations made when model error distributions used in the GzLM analysis were the same as those used in simulating *S–R* data. The REBs of α and β increased with an increase in sample sizes when normal errors were used in simulating *S–R* data. For other errors used in simulating data, they decreased as the sample size increased (Table 4). The RMSEs of α and β decreased with increasing sample size.

A comparison of Tables 3 and 4 indicates that percentages of the simulations with homogeneous residuals were always higher and REBs and RMSEs of α and β were always lower when the error assumptions used in the GzLM were the same as those used in simulating *S–R* data compared with those derived in the simulations when the model error distributions in the GzLM were not the same as the ones used in simulating data (Tables 3 and 4).

Different error assumptions in the GzLM yielded different estimates for the model parameters. Parameters estimated using lognormal and gamma distributions were similar, but parameters estimated using normal distribution in the GzLM were different from those estimated using lognormal and gamma distributions in the GzLM. Parameters estimated using a Poisson distribution tended to have values between those estimated using the normal error distribution versus lognormal and gamma distributions. Because this is a simulation study, we did not show the parameter estimate in every simulation. The trend of the mean error in total simulations can be observed from the REE and RMSE estimates (Fig. 2; Tables 3 and 4).

When the second *S–R* data (see Data simulation section) were used for the Cushing model, percentages of the simulations with homogeneous residuals were higher when the error distributions used in the GzLM were the same as those used in simulating *S–R* data (Table 5). Parameters estimated using the lognormal and gamma distributions were similar. Parameters estimated using the normal distribution in the GzLM differed from those estimated using the lognormal and gamma distributions. Parameters estimated using the Poisson distribution in the GzLM had values between those estimated using normal error and lognormal and gamma distributions in the GzLM. When the error distribution used in the GzLM was the same as that used in simulating *S–R* data, the percentages of the simulations with homogeneous residuals were higher and the REBs and RMSEs of α and β were smaller, and vice versa. This was consistent with the results derived for the first set of data, which had *S* values randomly drawn from 1000 to 10 000 values.

For the first set of data (randomly drawn *S* data) with outliers, when the error distributions used in the GzLM were the same as those used in simulating *S–R* data, the percentages of the simulations with homogeneous residuals decreased and the REBs and RMSEs of α and β increased with an increase in the number of outliers (Table 6). When the error distributions used in the GzLM were not the same as those used in simulating *S–R* data, the percentages of the simulations with homogeneous residuals increased with an increase in the number of outliers, if error distributions used in simulating *S–R* data were normal and error distributions used in the GzLM were lognormal and gamma. The same result could also be observed when the error distributions used in simulating *S–R* data were lognormal, gamma, and Poisson and the model errors used in the GzLM were normal. For other combinations of the distributions in simulating data and GzLM analyses, the percentages of simulations with ho-

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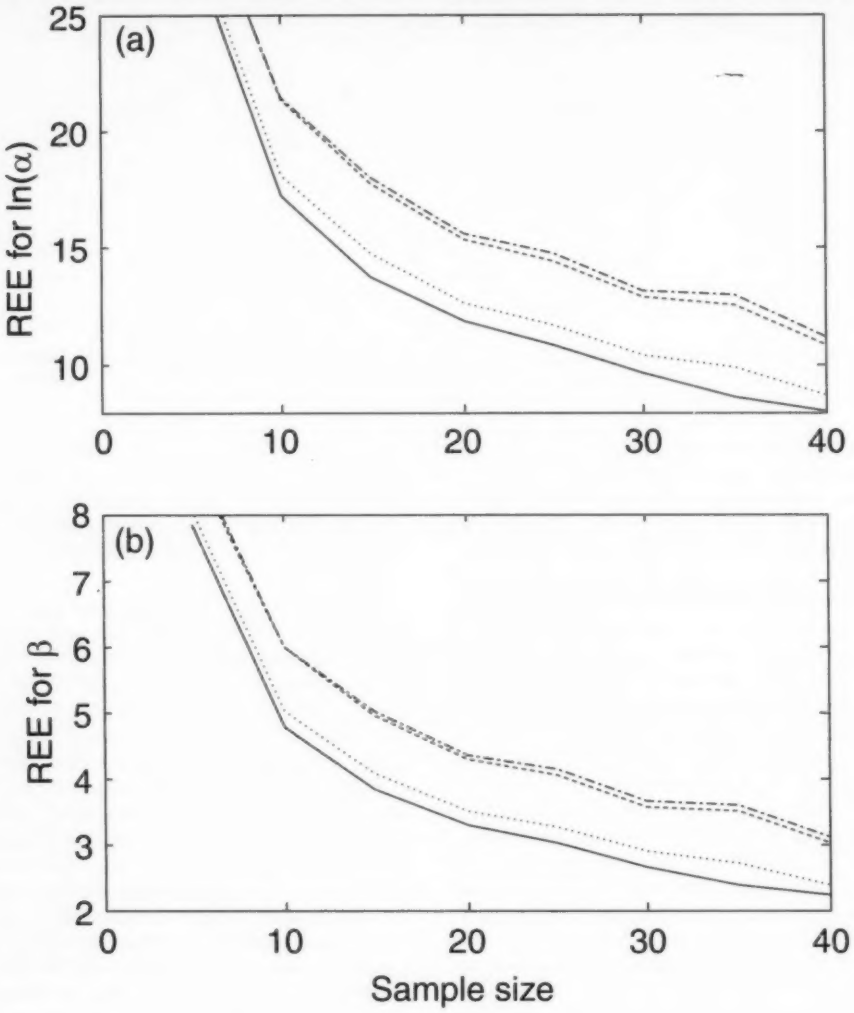
Fig. 2. Relative estimation error (REE) for the two parameters (*a*) ln(α) and (*b*) β in the Cushing model in 1000 simulation runs using different sample sizes in the simulation study. The simulated model error distribution is normal; the model error distributions used in the parameter estimates are normal (solid line), lognormal (dashed–dotted line), gamma (dashed line), and Poisson (dotted line).



mogeneous residuals decreased with an increasing number of outliers (Table 7). The REBs and RMSEs of α and β increased with an increase in the number of outliers in most cases (Table 7). Similar conclusions could be obtained when outliers were present in the second set of data simulated based on pink salmon *S* data (Tables 8 and 9).

When the Ricker and Beverton–Holt models were applied to data simulated under different scenarios, the results derived were consistent with those described above for the Cushing model. For brevity, the results for those two models are not shown in this paper.

Discussion

The regression method proposed for checking the residual homogeneity was effective in identifying homogeneous distributions of residuals. However, the effectiveness decreased with sample size. This was consistent with the fact that visual observation for residual homogeneity was difficult when sample sizes were small. This suggests that the regression method that we used in checking residual homogeneity of a large number of simulations was effective. However, we would suggest using the visual observation method in *S–R* modeling when there is only one set of residuals output.

The simulation results show that GzLM can help identify an appropriate model error distribution for parameter estimation through a residual homogeneity analysis. In most cases of the simulation, the true model error distribution used in the GzLM provided the highest percentage of simulation runs with homogeneous residuals. According to the simulation, this (i.e., the use of an appropriate error distributions in the GzLM) can improve the parameter estimation.

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Table 4. Summary of the simulations in which the model error distributions used in the generalized linear model analyses were not the same as those used in simulating stock–recruitment (*S–R*) data.

Model error distribution in simulating *S–R* data	in GzLM	No. of *S–R* observations	Simulations with homogeneous residuals (%)	REB for ln(α) (%)	REB for β (%)	RMSE for ln(α)	RMSE for β
Normal	Lognormal	20	26.3	2.57	0.70	0.4096	0.0486
		40	5.0	2.94	0.80	0.3033	0.0360
	Gamma	20	24.7	0.91	0.26	0.3999	0.0474
		40	4.6	0.84	0.23	0.2916	0.0346
	Poisson	20	55.5	0.31	0.09	0.3216	0.0378
		40	34.9	0.47	0.13	0.2315	0.0273
Lognormal	Normal	20	37.4	24.6	8.20	11.2407	1.2923
		40	13.1	5.25	3.02	2.2124	0.2666
	Gamma	20	81.8	4.39	0.45	2.0394	0.2480
		40	85.8	2.43	0.94	1.4105	0.1724
	Poisson	20	63.2	7.89	0.55	2.2546	0.2733
		40	43.9	2.72	0.85	1.5502	0.1890
Gamma	Normal	20	44.1	1.13	0.32	0.3392	0.0406
		40	17.8	0.20	0.05	0.2302	0.0277
	Lognormal	20	73.7	1.09	0.28	0.2924	0.0352
		40	64.2	0.09	0.01	0.1861	0.0224
	Poisson	20	72.6	0.85	0.24	0.2935	0.0353
		40	67.7	0.38	0.10	0.1915	0.0231
Poisson	Normal	20	58.6	0.041	0.012	0.0539	0.0064
		40	36.6	0.027	0.008	0.0367	0.0044
	Lognormal	20	58.5	0.046	0.013	0.0525	0.0063
		40	39.4	0.009	0.002	0.0371	0.0044
	Gamma	20	59.1	0.026	0.008	0.0525	0.0063
		40	37.9	0.016	0.005	0.0371	0.0044

Note: The Cushing model and the first set of data, which had *S* values randomly drawn from 1000 to 10 000 values, were used in the simulation. Relative estimate bias (REB) and root mean square error (RMSE) for parameters are shown. GzLM, generalized linear model; *S–R*, stock–recruitment.

Table 5. Summary of the simulations in which the Cushing model and the second set of data that had true *S* values of pink salmon were used in the simulation.

Model error distribution in simulating *S–R* data	in GzLM	Simulations with homogeneous residuals (%)	REB for ln(α) (%)	REB for β (%)	RMSE for ln(α)	RMSE for β
Normal	Normal	82.3	0.01	0.01	0.2144	0.0258
	Lognormal	26.9	2.18	0.59	0.3486	0.0425
	Gamma	31.1	0.37	0.10	0.3408	0.0415
	Poisson	59.6	0.01	0.01	0.2451	0.0296
Lognormal	Normal	37.1	7.86	0.80	2.8999	0.3556
	Lognormal	80.8	0.64	0.21	1.8501	0.2309
	Gamma	86.1	6.58	0.27	1.9416	0.2418
	Poisson	77.0	12.22	1.93	2.1647	0.2682
Gamma	Normal	32.8	0.43	0.12	0.3286	0.0405
	Lognormal	73.8	0.67	0.16	0.2644	0.0328
	Gamma	75.6	0.22	0.06	0.2636	0.0327
	Poisson	82.5	0.19	0.05	0.2639	0.0327
Poisson	Normal	53.0	0.011	0.003	0.0470	0.0058
	Lognormal	39.9	0.002	0.002	0.0472	0.0058
	Gamma	42.6	0.030	0.007	0.0472	0.0058
	Poisson	83.3	0.020	0.006	0.0417	0.0051

Note: Relative estimate bias (REB) and root mean square error (RMSE) for parameters were shown. GzLM, generalized linear model; *S–R*, stock–recruitment.

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Table 6. Summary of the simulation in which the model error distributions used in the generalized linear model analyses were the same as those used in simulating stock–recruitment (*S–R*) data.

Model error distribution in simulating *S–R* data	Distribution that outliers follow	Data being outliers (%)	Simulations with homogeneous residuals (%)	REB for ln(α) (%)	REB for β (%)	RMSE for ln(α)	RMSE for β
Normal	Lognormal	10	66.8	1.77	0.67	0.7189	0.0866
		20	58.4	2.28	0.97	1.1859	0.1477
		40	43.4	5.83	2.29	1.5351	0.1852
Lognormal	Normal	10	80.0	4.08	1.17	1.2193	0.1485
		20	81.6	0.36	0.09	1.1835	0.1444
		40	79.5	0.52	0.16	0.9844	0.1203
Gamma	Normal	10	55.2	0.14	0.03	0.2030	0.0244
		20	47.9	1.37	0.38	0.2273	0.0273
		40	29.0	0.16	0.04	0.2332	0.0278
Poisson	Normal	10	68.4	0.12	0.03	0.0780	0.0092
		20	69.5	0.13	0.04	0.1044	0.0123
		40	59.5	0.14	0.04	0.1499	0.0177

Note: The Cushing model and the first set of data, which had *S* values randomly drawn from 1000 to 10 000 values, were used in the simulation. Outliers were added and the sample size was 40. Relative estimate bias (REB) and root mean square error (RMSE) for parameters are shown.

Table 7. Summary of the simulation in which the model error distributions used in the generalized linear model analyses were not the same as those used in simulating stock–recruitment (*S–R*) data.

Model error distribution							
in simulating *S–R* data	in GzLM	Data being outliers (%)	Simulations with homogeneous residuals (%)	REB for ln(α) (%)	REB for β (%)	RMSE for ln(α)	RMSE for β
Normal	Lognormal	10	56.6	1.21	0.31	0.4658	0.0563
		20	69.8	1.69	0.46	0.6479	0.0788
	Gamma	10	56.0	1.03	0.12	0.5111	0.0619
		20	68.8	0.15	0.31	0.7147	0.0870
	Poisson	10	70.4	0.25	0.10	0.5843	0.0664
		20	68.3	0.38	0.24	0.7996	0.0972
Lognormal	Normal	10	18.9	3.21	0.51	1.9861	0.2385
		20	22.0	1.38	1.66	1.9122	0.2305
	Gamma	10	83.2	7.83	0.72	1.2994	0.1572
		20	83.0	4.04	0.20	1.2773	0.1557
	Poisson	10	49.1	9.25	1.13	1.4226	0.1724
		20	54.6	4.76	0.01	1.4020	0.1704
Gamma	Normal	10	23.3	0.19	0.05	0.2329	0.0279
		20	30.6	1.20	0.33	0.2283	0.0273
	Lognormal	10	56.4	0.78	0.19	0.2042	0.0245
		20	47.0	2.17	0.58	0.2325	0.0278
	Poisson	10	75.5	0.17	0.04	0.2001	0.0241
		20	78.1	1.15	0.32	0.2100	0.0252
Poisson	Normal	10	64.5	0.16	0.04	0.0730	0.0086
		20	71.2	0.13	0.04	0.0952	0.0112
	Lognormal	10	50.3	0.33	0.09	0.1017	0.0121
		20	42.4	0.34	0.09	0.1347	0.0160
	Gamma	10	47.6	0.08	0.02	0.0983	0.0117
		20	42.4	0.11	0.03	0.1317	0.0157

Note: The Cushing model and the first set of data, which had *S* values randomly drawn from 1000 to 10 000 values, were used in the simulation. Outliers were added and the sample size was 40. Relative estimate bias (REB) and root mean square error (RMSE) for parameters are shown. GzLM, generalized linear model.

This study suggests that the number of *S–R* data can greatly influence the effectiveness of identifying correct error distributions in the GzLM analyses and estimation errors. A small number of *S–R* data is likely to lead to low effectiveness in identifying homogeneous residuals and large estimation errors in *S–R* modeling. Thus, we should be cautious in using the GzLM when analyzing a small number of *S–R* data.

The presence of outliers can also impact a GzLM analysis in identifying a correct error distribution. When the number of outliers was 10% of the data, the percentage of simulation

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Table 8. Summary of the simulation in which the model error distributions used in the generalized linear model analyses were the same as those used in simulating stock–recruitment (*S–R*) data.

Model error distribution in simulating *S–R* data	Distribution that outliers follow	Data being outliers (%)	Simulations homogeneous residuals (%)	REB for ln(α) (%)	REB for β (%)	RMSE for ln(α)	RMSE for β
Normal	Lognormal	10	64.3	0.02	0.18	0.3168	0.0395
		20	40.2	18.44	11.32	3.1441	0.3871
		40	21.8	27.32	8.55	2.9112	0.3597
Lognormal	Normal	10	77.4	0.60	0.18	1.8214	0.2266
		20	67.3	4.57	1.29	1.5377	0.1895
		40	26.7	1.99	0.57	1.3729	0.1690
Gamma	Normal	10	76.2	0.22	0.06	0.2616	0.0323
		20	70.5	0.10	0.02	0.2411	0.0297
		40	61.0	0.63	0.18	0.2321	0.0286
Poisson	Normal	10	80.2	0.07	0.02	0.0590	0.0074
		20	69.1	0.08	0.02	0.1134	0.0142
		40	48.2	0.08	0.03	0.1209	0.0152

Note: The Cushing model and the second set of data that had true *S* values of pink salmon were used in the simulation. Outliers were added in simulating the data. Relative estimate bias (REB) and root mean square error (RMSE) for parameters are shown.

Table 9. Summary of the simulation in which the model error distributions used in the generalized linear model analyses were not the same as those used in simulating stock–recruitment (S–*R*) data.

Model error distribution							
in simulating *S–R* data	in GzLM	Data being outliers (%)	Simulations with homogeneous residuals (%)	REB for ln(α) (%)	REB for β (%)	RMSE for ln(α)	RMSE for β
Normal	Lognormal	10	83.2	1.71	0.43	0.5946	0.0760
		20	53.1	5.36	1.57	1.1047	0.1408
	Gamma	10	84.3	7.05	2.21	0.6534	0.0840
		20	53.5	18.04	5.66	1.2074	0.1549
	Poisson	10	73.8	4.05	1.33	0.4979	0.0641
		20	40.1	25.31	7.74	2.0522	0.2580
Lognormal	Normal	10	80.0	11.95	2.16	2.9611	0.3629
		20	86.1	41.40	10.64	1.3247	0.1527
	Gamma	10	82.1	14.52	2.72	1.9505	0.2412
		20	73.4	26.27	6.28	1.7398	0.2113
	Poisson	10	81.1	19.76	4.27	2.1775	0.2689
		20	85.7	35.73	9.03	1.4945	0.1772
Gamma	Normal	10	78.4	0.27	0.08	0.3213	0.0395
		20	83.0	0.07	0.03	0.1981	0.0241
	Lognormal	10	74.4	0.72	0.18	0.2617	0.0323
		20	69.3	0.67	0.16	0.2416	0.0297
	Poisson	10	84.2	0.09	0.03	0.2575	0.0318
		20	85.7	0.06	0.02	0.2004	0.0245
Poisson	Normal	10	65.7	0.14	0.04	0.0560	0.0068
		20	59.4	0.11	0.03	0.1596	0.0197
	Lognormal	10	87.7	0.05	0.02	0.0673	0.0085
		20	82.7	0.11	0.04	0.0870	0.0111
	Gamma	10	89.6	0.01	0.01	0.0671	0.0085
		20	82.5	0.03	0.01	0.0866	0.0110

Note: The Cushing model and the second set of data that had true *S* values of pink salmon were used in the simulation. Outliers were added when simulating the data. Relative estimate bias (REB) and root mean square error (RMSE) for parameters are shown. GzLM, generalized linear model.

runs with homogeneous residuals was highest when the correct error distributions were used in the GzLM analysis. When the number of outliers increased to 40%, the percentages of homogeneous residuals was no longer highest when the correct error distributions were used in the GzLM analysis. The normal error distribution tended to be more sensitive to outliers compared with the lognormal and gamma distributions. This study shows that even when the GzLM is less effective in identifying the correct error distribution with an increase in the number of outliers, the model error distribution used in the GzLM showing the highest percentage of simulation runs with homogeneous residuals usually pro-

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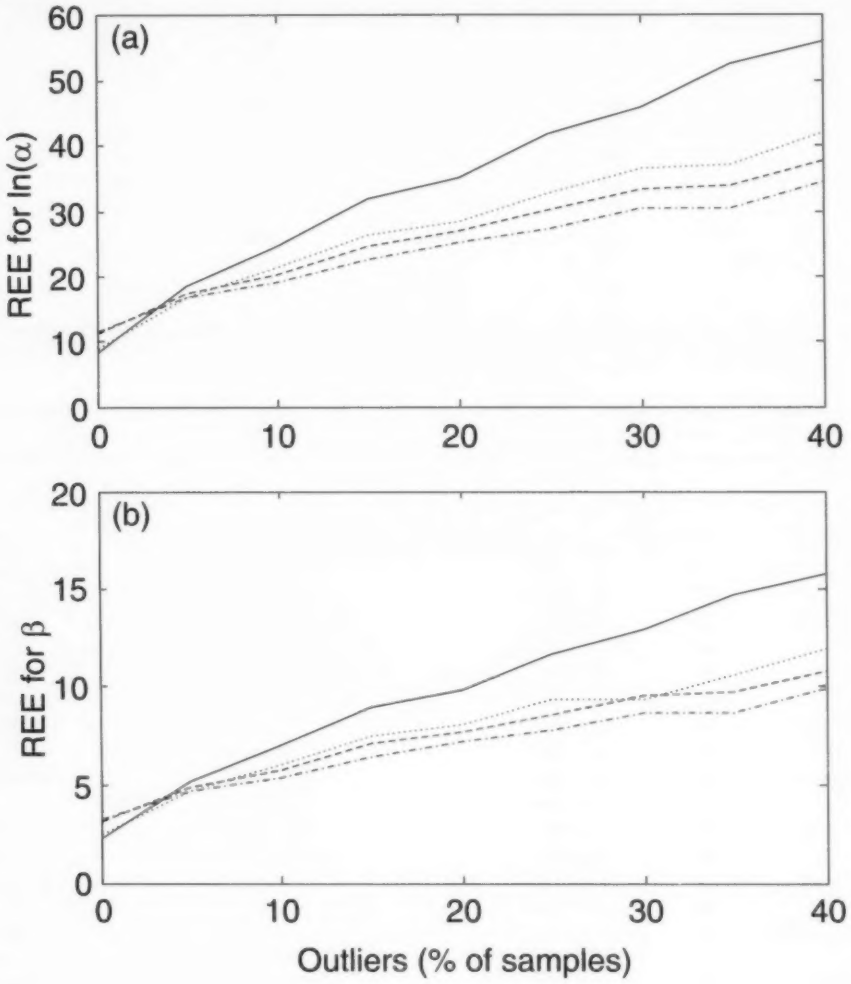
Fig. 3. Relative estimation error (REE) for the two parameters (*a*) ln(α) and (*b*) β in the Cushing model in 1000 simulation runs adding different percentages of outliers in the stock–recruitment data. The number of stock–recruitment observations used in the simulation is 40. The model error distribution used in simulating stock–recruitment data is normal; the model error distributions used in the generalized linear model for the parameter estimation are normal (solid line), lognormal (dashed–dotted line), gamma (dashed line), and Poisson (dotted line).



vides better parameter estimates with smaller REB and RMSE. We present an example (Fig. 3) illustrating the changes in estimation errors for ln(α) and β when different percentages of data were outliers. This suggest that the appropriate model error distribution may not be the underlying true error distribution because of the existence of outliers.

This study suggests that if the model error distribution used in simulating *S–R* data follows the Poisson distribution, then the parameters estimated using different error distributions in the GzLM have smaller differences. Thus, a Poisson-distributed error in *S–R* data is less sensitive to sample size, outliers, and choice of error distributions in the GzLM. The use of the Poisson distribution in the parameter estimation also showed robustness with respect to misspecification of error structure, small sample size, and outliers. For example, when the error distribution used in simulating *S–R* data was normal and the data were contaminated with lognormally distributed outliers, the Poisson error distribution used in the GzLM analysis provided the highest percentage of simulation runs with homogeneous residuals and better parameter estimates. Thus, we recommend using the Poisson distribution in a GzLM analysis of *S–R* data.

The simulated results did not show a clear difference when different *S–R* models were used. Because this is a simulation study and the data sets are based on "true" parameters with random errors, the performance of the models is difficult to compare.

We suggest the GzLM method be used to quantify *S–R* data relationships. The GzLM provides a convenient and effective way to evaluate and identify the appropriate model

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error distributions for a given set of data and models, leading to improved parameter estimation.

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An analysis of error structure in modeling the stock–recruitment data of gadoid stocks using generalized linear models

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Abstract: When modeling the stock–recruitment (*S–R*) relationship, the Cushing, Ricker, and other *S–R* models are fitted to the observed *S–R* data by estimating parameters with assumptions made concerning the model error structure. Using a generalized linear model approach, we explored and identified the appropriate model error structure in modeling *S–R* data for gadoid stocks. The *S–R* parameter estimation was found to be influenced by the choice of error distributions assumed in the analysis. In modeling *S–R* data for gadoid stocks, the Beverton–Holt model was found to be more sensitive to the assumption of model error distribution than the Cushing and Ricker models. The lognormal and gamma distributions had higher probability of being acceptable model error distributions. Cluster analyses and summary statistics of error distributions in *S–R* modeling did not show consistent patterns in the identification of an acceptable model error structure among species, geographic distributions, and sample sizes. A better understanding of the factors and mechanisms resulting in differences in the choice of appropriate model error distributions for different populations is needed in future research. We recommend that the generalized linear model be used to identify acceptable model error structures in quantifying *S–R* relationships.

Résumé : Lorsqu'on fait un modèle de la relation entre le stock et le recrutement (*S–R*), on ajuste les modèles de Cushing, de Ricker et les autres modèles *S–R* aux données observées en estimant des paramètres et en faisant des présuppositions sur la structure d'erreur du modèle. À l'aide d'une modèle linéaire généralisé, nous avons étudié et identifié la structure d'erreur du modèle appropriée à la modélisation de données *S–R* chez les stocks de gadoïdés. L'estimation du paramètre *S–R* est influencée par le choix des distributions d'erreurs présupposées dans l'analyse. Pour la modélisation des données *S–R* de stocks de gadoïdés, le modèle Beverton–Holt s'est révélé plus sensible au choix de distribution d'erreurs du modèle que les modèles de Cushing et de Ricker. Les distributions lognormale et gamma ont une plus forte probabilité d'être des distributions des erreurs du modèle acceptables. Des analyses de groupement et des statistiques générales des distributions d'erreurs dans les modèles *S–R* n'indiquent pas de patterns constants dans l'identification d'une distribution d'erreurs du modèle acceptable en fonction des espèces, des répartitions géographiques et des tailles d'échantillons. Il sera nécessaire, dans les recherches futures, d'obtenir une meilleure compréhension des facteurs et des mécanismes responsables des différences dans le choix de distributions d'erreurs du modèle appropriées aux différentes populations. Nous recommandons d'adopter le modèle linéaire généralisé pour identifier les structures d'erreurs du modèle acceptables lorsqu'on quantifie les relations *S–R*.

[Traduit par la Rédaction]

Introduction

Many species in the family Gadidae, such as *Gadus morhua* in the North Atlantic and *Theragra chalcogramma* in the North Pacific, have high economic values. Information on their future recruitments, which is commonly estimated from the corresponding spawning stock biomass, is critical for their management (Hilborn and Walters 1992). Large variations of recruitment have been observed in many cod stocks (e.g., Myers et al. 1995; Myers and Barrowman 1996; Hinrichsen 2001). Understanding the dynamics of recruitment requires full understanding of the dynamics of spawning stock biomass (Ricker 1975). Knowledge of the stock–recruitment (*S–R*) relationship is commonly obtained through quantitative modeling. The *S–R* relationship of cod stocks has been explored in many studies (e.g., Myers et al. 1995; Myers and Barrowman 1996; Power 1996). However, as noted by Hilborn and Walters (1992), the estimation of the *S–R* relationship is perhaps the most difficult work in fisheries stock assess-

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ment. For many fish stocks, the *S–R* relationships are not clear (Ricker 1975; Hilborn and Walters 1992; Iles 1994). The shape of the recruitment curve is often hard to determine because of small sample size and high variability in recruitment.

A combination of the assumed model form and error structure determines an objective function, which in turn dictates the parameter estimation (Chen et al. 2003). The lack of fit of data to an *S–R* model does not necessarily establish the independence between the stock and recruitment. It likely results from a highly skewed distribution of recruitment values for a given level of stock (Chen and Paloheimo 1995). Thus understanding the model error structure is necessary in evaluating and estimating the relation of recruitment to stock size.

Modeling errors result from inappropriate model form or inappropriate error structure (Carroll and Ruppert 1984; Schnute 1991; Schnute and Richards 2001). Different mathematical functions have been developed for the *S–R* models based on ecological and mathematical theories (Hilborn and Walters 1992). The model error structure is often ignored in the *S–R* model fit. For example, in fitting a *S–R* model using a nonlinear least-squares method, the assumed model error distribution is always normal. A commonly used practice is to linearize *S–R* models by taking an appropriate transformation (e.g., logarithmic for the Cushing and Ricker models; reciprocal for the Beverton–Holt model) and then to use a least-squares criterion to estimate parameters. The intrinsic recruitment distribution has often been ignored for the convenience of parameter estimation, perhaps resulting in estimation errors (Chen and Paloheimo 1995).

The necessity of having a realistic error structure or applying an estimation method that is robust to the error structure assumption in modeling the dynamics of fish populations has been discussed in various studies (Bajdik and Schneider 1991; Chen and Paloheimo 1998; Shertzer and Prager 2002). In this paper, we used a generalized linear model method to explore and identify acceptable error structures in modeling *S–R* data for cod stocks. The generalized linear model method is a maximum likelihood based method that provides a convenient and effective way to evaluate and identify the acceptable model error distribution for given data and models. The choice of the link function, which is an essential component in the generalized linear model method, does not affect the assumptions concerning the distribution of the independent variable, unlike the case of transformations used in least-squares methods (Bajdik and Schneider 1991; Quinn and Deriso 1999). In an extensive Monte Carlo simulation study, Jiao et al. (2004) found that the quality of *S–R* parameter estimates, measured by estimation errors, could be influenced by the realism of error structure assumed in an estimation, the number of *S–R* data points, and the number of outliers in modeling. A small number of *S–R* data points and the presence of outliers in *S–R* data could increase the difficulty of identifying the appropriate error structure in modeling, which might lead to large biases in *S–R* parameter estimation. They also found that the generalized linear model could help identify the acceptable error distribution in *S–R* modeling, leading to an improved estimation of parameters even when there were outliers and the number of *S–R* data points was small (Jiao et al. 2004).

In this study, using the generalized linear model method, we explore and identify acceptable model error structures for commonly used Cushing, Ricker, and Beverton–Holt models in fitting the *S–R* data of gadoid stocks. Four model error distributions (normal, lognormal, gamma, and Poisson) were used in this study. The normal distribution is widely used in assuming error distributions for biological and fishery variables in fisheries modeling, which results from an assumption that environmental variations are random. Because of large environmental changes or other reasons, the variations of those variables might be skewed. Even when both recruitment and stock size follow normal distributions, the model error might not be normal (Chen and Paloheimo 1995). We therefore included the skewed distributions of lognormal and gamma in this study. We also included the Poisson distribution because the recruitment is nonnegative count data. The use of the Poisson distribution in the parameter estimation also showed robustness with respect to misspecification of error structure, small sample size, and outliers in our simulation study (Jiao et al. 2004). For example, when the error distribution used in simulating *S–R* data was normal and the data were contaminated with lognormally distributed outliers, the Poisson error distribution used in the generalized linear model analysis provided the highest percentage of simulation runs with homogeneous residuals and better parameter estimates (Jiao et al. 2004).

We evaluated all cod stocks for which *S–R* data are available to determine whether there were consistent patterns among different gadoid stocks in identifying acceptable *S–R* model error distributions.

Materials and methods

The *S–R* data used in this study are cod stocks in the family Gadidae obtained from Dr. R.A. Myers's website at http://www.mscs.dal.ca/~myers/welcome.html. The fishery divisions and the data sources are shown in Dr. Myers's website and in Myers et al. (1995). The stocks in the North Atlantic generally follow the divisions of the Northwest Atlantic Fisheries Organization (NAFO) or the International Council for the Exploitation of the Sea (ICES) (Fig. 1). Some of the stocks are called by the location name if they are commonly applied to the stocks in practice or if the NAFO or ICES regions do not adequately describe the presently used stock boundaries (Myers et al. 1995). For the Atlantic cod (*Gadus morhua*) stock in NAFO divisions 2J3KL, we updated the *S–R* data to the year 1997 using catch data (Lilly et al. 2001) and sequential population analysis. Updated *S–R* data from NAFO division 3Ps were estimated based on the data from Brattey et al. (2001).

In this study, we analyzed the *S–R* relationship based on the Cushing, Ricker, and Beverton–Holt models (Quinn and Deriso 1999) to explore the identification of acceptable *S–R* model error distributions in cod stocks. The Cushing model can be written as

$$(1) \qquad R = \alpha S^{\beta}$$

the Ricker model can be written as

$$(2) \qquad R = \alpha S e^{-\beta S}$$

and the Beverton–Holt model can be written as

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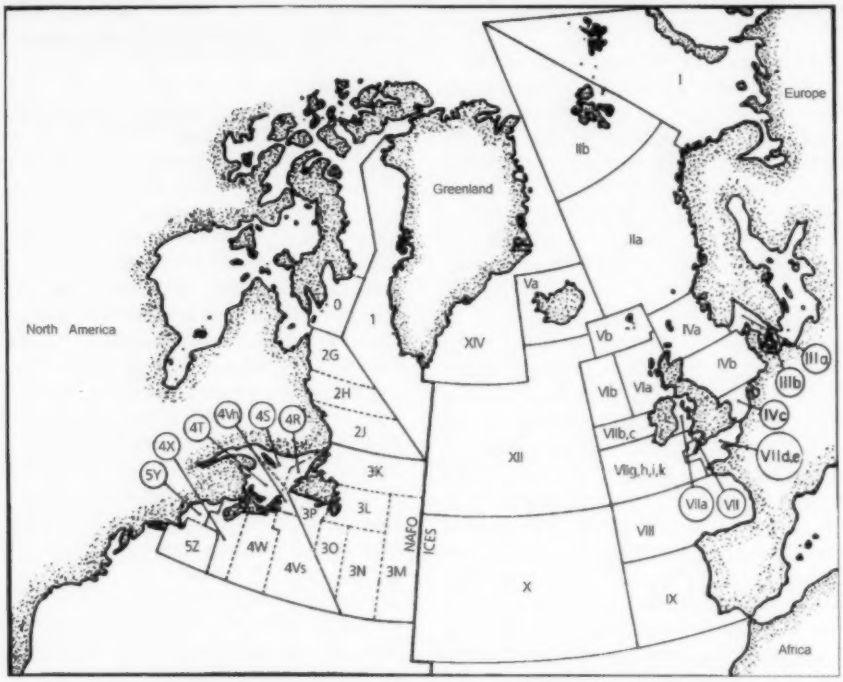
Fig. 1. A map of the North Atlantic on an azimuthal equal area projection centered at 40°N and 35°W, showing the North Atlantic Fisheries Organization (NAFO) areas off the eastern coast of North America and International Council for the Exploration of the Sea (ICES) areas (modified from Charles 2001).



$$R = \alpha S/(1 + \beta S) \quad (3)$$

where α and β are two parameters to be estimated, and S and R are the spawning stock biomass and its subsequent recruitment, respectively.

The generalized linear model was used to explore the model error distributions. This model is sometimes abbreviated as GLM (McCullagh and Nelder 1989; Lindsey 1997; Myers et al. 2001), GLIM (software distributed by Numerical Algorithms Group Ltd., Oxford, U.K.), or GLZ (StatSoft Inc., Tulsa, Okla.), but in this paper, we write GzLM to differentiate the generalized linear model from the general linear model (GLM) and the software GLIM.

The procedure of GzLM parameter estimation for the Cushing, Ricker, and Beverton–Holt models was detailed in Jiao et al. (2004). Following that study, we used the following procedure to determine whether an assumed error structure was acceptable for a given set of *S–R* data and *S–R* model. An *S–R* model is fitted to an *S–R* data set by assuming an initial error distribution to estimate the model parameters. Pearson residuals (McCullagh and Nelder 1989) from the model fitting were calculated. Pearson residuals are the differences between observed and predicted values, standardized (divide by the estimated standard deviation of the fitted value) to make their variance (theoretically) constant. The Pearson residuals were first used to check for the homogeneity of model error distributions. Visual checking was used by looking at the plot of the Pearson residuals against fitted values. For a given *S–R* model and set of data, we selected acceptable model error distributions according to variance diagnostic analyses (see Fig. 1 in Jiao et al. 2004). An assumed model error distribution in *S–R* modeling resulting in homoscedastic residuals was regarded as an acceptable model error distribution, and vice versa (McCullagh and Nelder 1989). Because the *S–R* data points are not averagely distributed in many of the data sets and because some of the *S–R* data sets have small sample size, it is subjectively biased when visual checking is used based on the Pearson residuals against fitted values. This is the main criterion used to diagnose the residuals. Normal probability plot is used as the second step in diagnosing the residuals. A disadvantage of the Pearson residual is that the distribution of Pearson residuals for nonnormal distribution is often markedly skewed and so may fail to have properties similar to those of a normal-theory residual. Anscombe residuals (McCullagh and Nelder 1989) improved the normal theory characteristics to a degree. It normalized the probability functions and stabilized the variance through transformations (McCullagh and Nelder 1989). In this study, Anscombe residuals were also used to diagnose the model error. When an acceptable model error distribution is used in the generalized linear model, the normal probability plot of the Anscombe residuals will show normal probability characteristics, i.e., the normal probability plot of the Anscombe residuals will be linear. As an example, the *S–R* data from Dr. Myers' website for cod (*G. morhua*) from NAFO divisions 2J3KL were analyzed using the three *S–R* models with four types of model error distributions assumed in estimating parameters in the *S–R* models (Table 1).

We used a cluster analysis to identify the similarities, grouping patterns among species and (or) stocks based on their error distributions observed in *S–R* modeling using the

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Table 1. Stock–recruitment parameter estimates for Atlantic cod (*Gadus morhua*) stock in North Atlantic Fisheries Organization (NAFO) divisions 2J3KL when the four different model error distributions were used in the generalized linear model (GzLM).

Model	Error distribution	Parameter estimate from GzLM		
		α	β	R^2
Cushing	Normal	430.8880	1.0592	0.7374
	Lognormal	4918.7063	0.6600	0.6757
	Gamma	9632.7740	0.5832	0.6598
	Poisson	2500.9341	0.7978	0.7008
Ricker	Normal	649.2384	1.000×10^{-7}	0.7304
	Lognormal	719.5640	2.5091×10^{-4}	0.6808
	Gamma	1072.9489	5.2325×10^{-4}	0.5880
	Poisson	730.4731	1.0673×10^{-4}	0.7127
Beverton–Holt	Normal	649.2401	2.5423×10^{-5}	0.7304
	Lognormal	800.3312	8.0680×10^{-6}	0.6565
	Gamma	1353.1077	7.7507×10^{-6}	0.5665
	Poisson	2849.6326	1.6283×10^{-5}	0.3899

GzLM. We used a sequential, agglomerative, hierarchical algorithm based on the Manhatten distance in the cluster analysis (Everitt et al. 2001). This means that in the hierarchical clustering, the agglomerative method was used. Here we used the average linkage (UPGMA) to do the agglomerative hierarchical clustering. The distance used in the clustering analysis is the Manhatten distance. Species and stocks listed in Tables 2 and 3 are clustered according to their acceptable *S–R* Cushing, Ricker, and Beverton–Holt model error distributions identified in the GzLM.

Results

The parameter estimates varied with the error distribution assumed in the GzLM estimation for cod of NAFO divisions 2J3KL, which was used as an example in this study (Table 1). The residual diagnostic plots for the Cushing model did not clearly show which error distribution yielded homogeneous residuals, but the residual diagnostic plots look better when normal and Poisson distributions were used than when lognormal and gamma distributions were used (Fig. 2). The normal probability plot of Anscombe residuals clearly showed that the normal error distribution yielded normal residuals, whereas the Poisson distribution assumptions were less acceptable (Fig. 3). Combining the above diagnoses, the normal distribution was regarded as the acceptable model error structure. When the four model error distributions were assumed in the GzLM for the Cushing model, the parameter estimates and model fits differed greatly (Table 1; Fig. 4). We show parameter estimates when the four model error distributions were assumed in the GzLM for the Ricker and Beverton–Holt models but do not show residual diagnostic plots and normal probability plots (Table 1). The estimation procedure and the residual diagnostic procedure are the same when determining an acceptable model error distribution.

When the *S–R* data for the 17 Gadidae species (86 stocks) were analyzed based on the Cushing, Ricker, and Beverton–Holt models using the GzLM, the acceptable model error distributions were found to depend on the stocks and choice of the models (Tables 2 and 3). A comparison of the acceptable model error distributions in using data from Dr. Myers' website with the updated *S–R* data for cod stocks from NAFO divisions 2J3KL and 3Ps (Table 2) suggested that the identification of acceptable model error distributions in GzLM was also related to sample size or the years included in the analysis. There were stocks for which several model error distributions were acceptable for the *S–R* models (e.g., GM20, MM47). There were also stocks for which none of the four error distributions included in this study was acceptable for a *S–R* model (e.g., GMP2, MG60).

The proportion of the *G. morhua* stocks for which an acceptable model error distribution could be identified (Table 2) was similar to that for all stocks analyzed (Table 3). The lognormal distribution was acceptable in 52% of the cases when the Cushing model was used, in 57% of the cases when the Ricker model was used, and in 48% of the cases when the Beverton–Holt model was used for the 86 gadoid stocks (Table 3). They were 50%, 62%, and 47%, respectively, for the 34 *G. morhua* stocks (Table 2). The gamma distribution was ranked second by number and percentage for being identified as an acceptable model error distribution in the analyses. The gamma distribution was acceptable in 36% of the cases when the Cushing model was used, in 33% of the cases when the Ricker model was used, and in 37% of the cases when the Beverton–Holt model was used for all gadoid stocks. They were 35%, 32%, and 41%, respectively, for 34 *G. morhua* stocks. The number of acceptable model error distributions for the Cushing model was slightly more than that for the Ricker and Beverton–Holt models. The numbers of the normal, lognormal, gamma, and Poisson distributions being identified as acceptable model error distributions were similar for all Cushing, Ricker, and Beverton–Holt models (Tables 2 and 3).

The 34 *G. morhua* stocks could be divided into two groups according to the cluster analysis of the error distributions observed in *S–R* modeling using the GzLM (Fig. 5). Group 1 included stocks that had only lognormal and (or) gamma model error distributions identified acceptable in the GzLM analysis of *S–R* data for a given *S–R* model. Among these stocks, in subgroup 1A, only the lognormal and (or) gamma distribution were identified as acceptable error distributions in the GzLM analysis of the three *S–R* models, except in stock GM32 where the Poisson distribution was identified as

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Table 2. *Gadus morhua* stocks and their acceptable stock–recruitment model error distributions identified in the generalized linear model (GzLM) for the Cushing, Ricker, and Beverton–Holt models.

				Cushing model				Ricker model				Beverton–Holt model			
Stock	Code	Fishery distribution	Sample size	N	L	G	P	N	L	G	P	N	L	G	P
Baltic areas 22 and 24	GM3	NEA	22	1	0	1	0	1	0	1	0	1	0	1	0
Baltic areas 25–32	GM4	NEA	24	0	1	1	0	0	1	1	0	0	1	1	0
Celtic Sea	GM5	NEA	22	0	1	0	0	0	1	0	0	0	1	0	0
Faroe Plateau	GM6	NEA	33	0	0	1	0	0	1	0	0	0	0	1	0
Flemish Cap (NAFO 3M) 1	GM7	NWA	9	0	0	0	1	0	0	1	1	0	0	1	1
Flemish Cap (NAFO 3M) 2	GM8	NWA	27	0	0	1	0	0	0	1	0	0	0	1	0
Greenland offshore component	GM9	NEA	35	0	1	0	0	0	1	0	0	0	1	0	0
ICES VIId	GM10	NEA	18	0	1	0	0	0	1	0	0	0	1	0	0
ICES VIa	GM11	NEA	27	0	1	1	0	0	1	1	0	0	1	1	0
Iceland	GM12	NEA	68	0	1	0	0	0	1	0	0	0	1	0	0
Irish Sea	GM13	NEA	27	0	0	1	0	0	1	0	0	0	0	1	0
Kattegat	GM14	NEA	21	1	0	0	0	1	0	0	0	0	0	0	1
NAFO 2J3KL	GM15	NWA	28	1	0	0	0	1	0	0	0	0	0	0	1
NAFO 2J3KL updated	N_2J	NWA	36	1	0	0	1	1	0	0	1	0	0	0	1
NAFO 3M	GM16	NWA	10	0	0	0	0	0	1	1	0	0	0	1	0
NAFO 3NO	GM17	NWA	31	0	0	1	0	0	0	1	0	0	0	1	0
NAFO 3Pn4RS 1	GM18	NWA	17	0	0	0	0	0	1	1	0	0	0	0	0
NAFO 3Pn4RS 2	GM19	NWA	21	0	1	1	0	0	1	1	0	0	1	1	0
NAFO 3Ps	GM20	NWA	31	1	1	1	1	1	1	1	1	1	1	1	1
NAFO 3Ps updated	N_3Ps	NWA	41	1	0	0	1	1	0	0	1	1	0	0	1
NAFO 4TVn	GM21	NWA	41	1	0	1	1	1	1	0	0	1	0	1	1
NAFO 4VsW	GM22	NWA	33	1	0	0	1	1	0	0	1	1	0	0	1
NAFO 4X	GM23	NWA	45	0	0	1	0	0	0	0	0	0	0	1	0
NAFO 5Y 1	GM24	NWA	7	0	0	0	0	0	0	0	0	0	0	0	0
NAFO 5Y 2	GM25	NWA	34	0	1	0	0	0	1	0	0	0	1	0	0
NAFO 5Z 1	GM26	NWA	20	0	1	0	0	0	1	0	0	0	1	0	0
NAFO 5Z 2	GM27	NWA	34	0	1	0	0	0	0	0	0	0	0	0	0
Northeast Arctic 1	GM28	NEA	43	0	1	0	0	0	1	0	0	0	1	0	0
Northeast Arctic 2	GM29	NEA	45	0	1	0	0	0	1	0	0	0	1	0	0
Northeast Arctic 3	GM30	NEA	59	0	1	0	0	0	1	0	0	0	1	0	0
Northeast Arctic 4	GM31	NEA	59	1	0	0	0	1	0	0	1	1	0	0	1
North Sea	GM32	NEA	30	0	1	1	1	0	1	1	0	0	1	1	0
Skagerrak	GM33	NEA	13	0	1	0	0	0	1	0	0	0	1	0	0
West Greenland (NAFO 1)	GM34	NWA	35	0	1	0	0	0	1	0	0	0	1	0	0
Total				9	17	12	7	9	21	11	6	6	16	14	9
Proportion				0.26	0.50	0.35	0.21	0.26	0.62	0.32	0.18	0.18	0.47	0.41	0.26

Note: The stocks generally follow the Northwest Atlantic Fisheries Organization (NAFO) or the International Council for the Exploitation of the Sea (ICES) divisions or the commonly used name based on their distribution. N, L, G, and P represent normal, lognormal, gamma, and Poisson distribution, respectively. Zero (0) indicates an unacceptable model error distribution and one (1) indicates an acceptable model error distribution. The fishery distribution areas are classified as Northeast Atlantic (NEA) and Northwest Atlantic (NWA).

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Fig. 2. Diagnostic plots of Pearson residuals using the four types of model error distributions in the generalized linear model (GzLM) to estimate the parameters in the Cushing model for Atlantic cod (*Gadus morhua*) stock in the North Atlantic Fisheries Organization (NAFO) divisions 2J3KL. The four model error distributions are (*a*) normal distribution (note that the *y* axis in this panel is $\times 10^5$), (*b*) lognormal distribution, (*c*) gamma distribution, and (*d*) Poisson distribution.

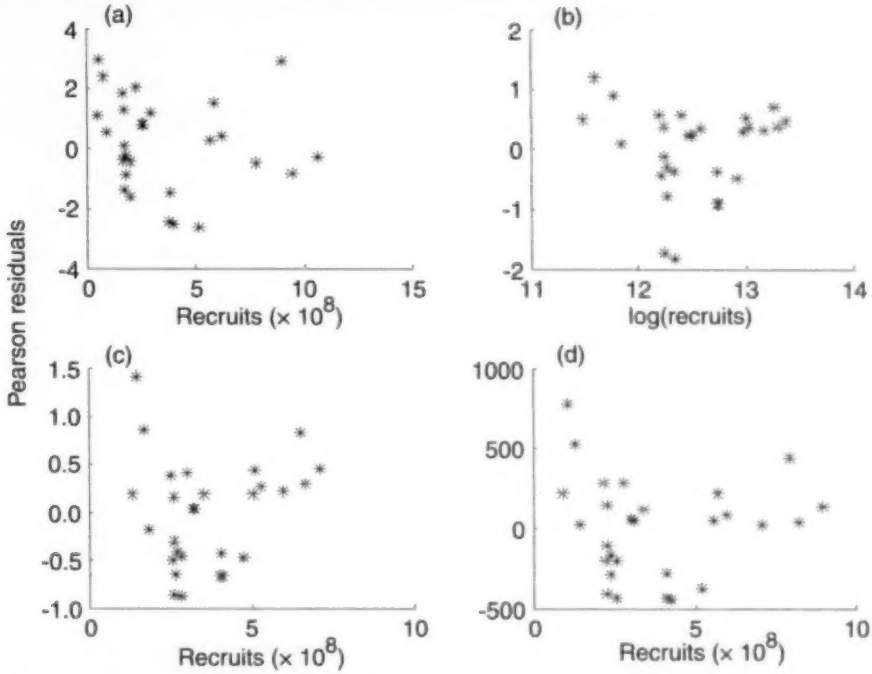

Fig. 3. Normal probability plot of Anscombe residuals used to diagnose the four types of model error distributions used in the generalized linear model (GzLM) to estimate the parameters in the Cushing model for Atlantic cod (*Gadus morhua*) stock in the North Atlantic Fisheries Organization (NAFO) divisions 2J3KL. The four model error distributions are (*a*) normal distribution (note that the *x* axis in this panel is $\times 10^8$), (*b*) lognormal distribution, (*c*) gamma distribution, and (*d*) Poisson distribution.

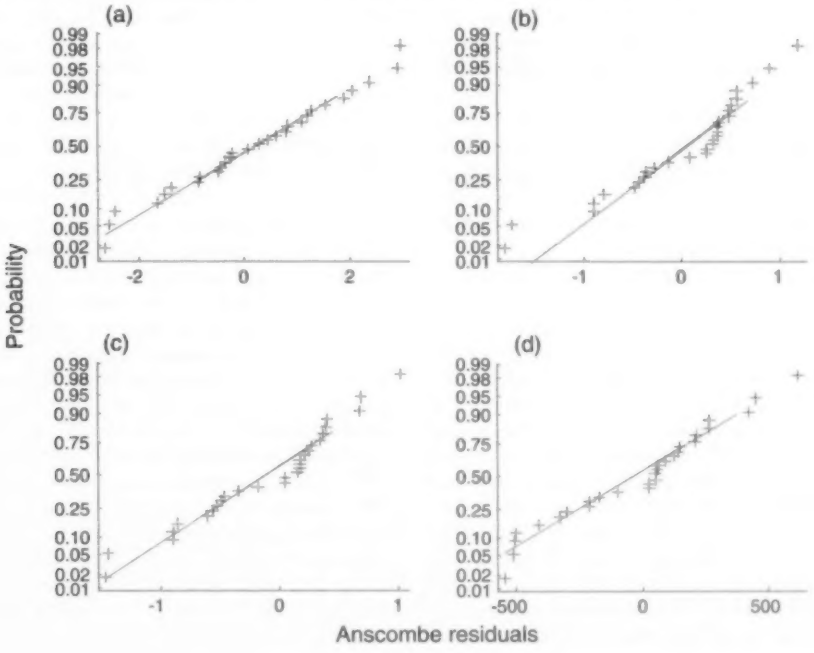

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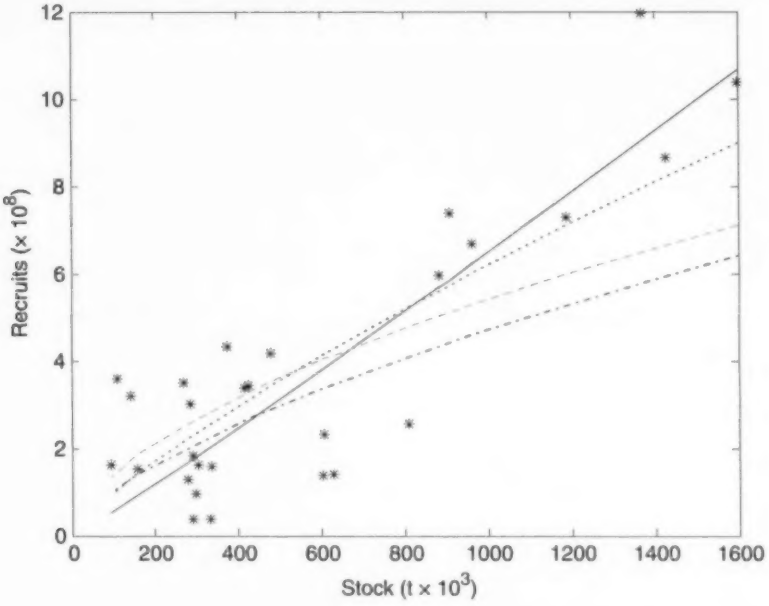
Fig. 4. Regression analyses when the four types of model error distributions were used in the generalized linear model (GzLM) to estimate the parameters in the Cushing model for Atlantic cod (*Gadus morhua*) stock in the North Atlantic Fisheries Organization (NAFO) divisions 2J3KL. Observed data (stars), normal (solid line), lognormal (dashed–dotted line), gamma (dashed line), and Poisson (dotted line).



an acceptable error distribution in the Cushing model. For stocks in subgroup 1B, only the lognormal distribution was identified as an acceptable error distribution in the GzLM analysis of the three *S–R* models, except in stock GM24 where none of the distributions was identified as an acceptable error distribution in the all three *S–R* models and in stock GM27 where none of the distributions was identified as an acceptable error distribution in the Ricker and Beverton–Holt models. For stocks in subgroup 2B, the normal and (or) Poisson distributions were identified as the acceptable model error distributions in the GzLM analysis of *S–R* data, except in stock GM7 where the gamma distribution was identified as an acceptable error distribution in the Ricker and Beverton–Holt models. Stocks in subgroup 2A differed from those in groups 1 and 2B in that multiple error distributions were identified as acceptable in the GzLM analysis of *S–R* data for the *S–R* models.

All gadoid stocks could be divided into three groups according to the cluster analysis of the *S–R* modeling errors in the GzLM (Fig. 6). Groups 1 and 3 were composed of stocks for which all three *S–R* models had one or two error distributions that could be defined as acceptable in the GzLM. Group 2 was mainly composed of stocks for which the *S–R* models had multiple error distributions that could be defined as acceptable in the GzLM. For subgroup 1A1, the acceptable *S–R* modeling error distributions were none or only one in one of the *S–R* models. In stocks GM27 and TC80, only lognormal distribution was acceptable in the Cushing model in the GzLM analysis. In stocks MA39, MG61, and TC76, only lognormal distribution was acceptable in the Ricker model. In stocks MA53 and TC77, only Poisson distribution was acceptable in the Beverton–Holt model and in the Ricker model separately. Subgroup 1A2 was composed of the stocks for which only lognormal error distribution was acceptable in most of the cases. In subgroup 1A2A, the acceptable *S–R* model error distribution was only lognormal in all three *S–R* models. For all stocks in subgroup 1C, the lognormal and (or) gamma error distributions were the acceptable model error distributions. Subgroup 1C2 was composed of the stocks for which only gamma error distribution was acceptable in most of the cases. In subgroup 3A, the Poisson and (or) gamma error distributions were acceptable. In subgroup 3B, the stocks had normal and (or) Poisson distributions as the acceptable *S–R* model error distributions. In other subgroups, the *S–R* models of the stocks had multiple acceptable model error distributions or no common features in the acceptable model error distributions.

The grouping based on the cluster analyses of *S–R* modeling errors (i.e., residuals) did not show a clear pattern among species and (or) stocks, geographic distributions, and sample sizes (Figs. 5 and 6). For stocks with sample sizes ≤15, the lognormal distribution had the highest probability of being defined as an acceptable model error structure for the Cushing and Ricker models, but in the Beverton–Holt model, the gamma distribution had the same proportion as the lognormal distribution. As the sample size increased to >15, the lognormal distribution had the highest probability of being defined as an acceptable model error distribution in all three *S–R* models, but the proportion of the stocks for which lognormal or gamma was identified as acceptable in the GzLM decreased when the sample size increased to >30 (Table 4). From the total value of the proportion of the stocks for which a particular model error distribution was identified as acceptable in the GzLM analysis, the number of acceptable

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Table 3. Gadidae species and stocks (except *Gadus morhua*) and their acceptable stock–recruitment model error distributions identified in the GzLM.

				Cushing model				Ricker model				Beverton–Holt model			
Species and stocks	Code	Fishery distribution	Sample size	N	L	G	P	N	L	G	P	N	L	G	P
Gadus macrocephalus (Pacific cod)															
Eastern Bering Sea	GMP1	NEP	10	0	1	1	0	0	0	1	1	0	1	1	0
Hecate Strait	GMP2	NEP	14	0	0	0	0	0	0	0	0	0	0	0	0
Melanogrammus aeglefinus (Haddock)															
Faroe Plateau	MA35	NEA	33	0	0	0	1	0	0	0	1	0	0	0	1
ICES VIa	MA36	NEA	29	0	1	0	0	0	1	0	0	0	1	0	0
Iceland	MA37	NEA	28	0	0	1	0	0	0	1	0	0	0	1	0
NAFO 4TVW	MA38	NWA	38	0	1	0	0	0	1	0	0	0	0	0	0
NAFO 4X 1	MA39	NWA	24	0	0	0	0	0	1	0	0	0	0	0	0
NAFO 4X 2	MA40	NWA	26	1	0	0	0	1	0	0	1	1	0	0	0
NAFO 5Z	MA41	NWA	68	0	0	1	0	0	0	1	0	0	0	1	0
Northeast Arctic	MA42	NEA	44	0	0	1	0	0	0	1	0	0	0	1	0
North Sea 1	MA43	NEA	32	0	0	1	0	0	0	0	0	0	0	1	0
North Sea 2	MA44	NEA	66	0	1	0	0	0	1	0	0	0	1	0	0
Rockall Bank	MA45	NEA	9	1	0	0	0	0	1	0	0	0	0	1	1
Merlangius merlangus (Black Sea whiting)															
Eastern Black Sea	MM46	NEA	24	0	1	0	0	0	1	0	0	0	1	0	0
Western Black Sea	MM47	NEA	23	1	1	1	1	1	1	1	1	1	1	1	1
Merlangius merlangus (whiting)															
Celtic Sea	MM48	NEA	9	0	1	0	0	0	1	0	0	0	1	0	0
ICES VIId	MM49	NEA	14	1	0	0	1	1	0	0	0	1	0	0	1
ICES VIa	MM50	NEA	27	0	1	0	0	0	1	0	0	0	1	0	0
Irish Sea	MM51	NEA	13	0	0	0	0	1	1	1	1	0	0	0	0
North Sea 1	MM52	NEA	27	0	1	1	0	0	1	1	0	0	1	0	0
North Sea 2	MM53	NEA	74	0	0	0	0	0	0	0	0	0	0	0	1
Merluccius bilinearis (silver hake)															
Mid-Atlantic Bight	MB54	NEA	33	0	1	0	0	0	1	0	0	0	1	0	0
NAFO 4VWX	MB55	NWA	13	0	1	1	0	0	1	1	0	0	1	1	0
NAFO 5Ze	MB56	NWA	33	0	0	0	1	0	0	0	1	0	0	0	1
Merluccius capensis (Cape hake)															
South Africa 1.6	MC57	SEA	20	0	1	0	0	0	0	0	0	0	1	0	0
South Africa South Coast	MC58	SEA	12	0	0	0	0	0	0	0	0	0	0	0	0
Merluccius gayi (Peruvian hake)															
Chile – South Central zone	MG59	SEA	14	1	0	0	1	1	0	0	1	0	0	0	0
Chile – Northern zone	MG60	SEA	14	0	0	0	0	0	0	0	0	0	0	0	0
Peru documentation	MG61	SEA	8	0	0	0	0	0	1	0	0	0	0	0	0
Merluccius merluccius (European hake)															
ICES VIIIa,b,d, VIIb–k	MMH62	NEA	20	1	1	1	1	1	1	1	1	1	1	1	1
ICES VIIIc and IXa	MMH63	NEA	16	1	1	1	1	1	1	1	1	1	1	1	1
Jabuka Pit, Adriatic Sea	MMH64	NEA	26	0	0	0	1	1	0	0	1	1	0	0	1
Southwest Atlantic Ocean	MMH65	SWA	9	1	1	1	1	1	1	1	1	1	1	1	1

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Table 3 (*concluded*).

Species and stocks	Code	Fishery distribution	Sample size	Cushing model				Ricker model				Beverton–Holt model			
				N	L	G	P	N	L	G	P	N	L	G	P
Merluccius productus (Pacific hake)															
Western U.S. + Canada	MP66	NEP	23	0	1	0	0	0	1	0	0	0	1	0	0
Micromesistius australis (southern blue whiting)															
Campbell Island, N.Z.	MA67	SWP	14	0	1	0	0	0	1	0	0	0	1	0	0
Micromesistius poutassou (blue whiting)															
Northern ICES	MPB68	NEA	20	0	1	0	0	0	1	0	0	0	1	0	0
Southern ICES	MPB69	SEA	10	1	1	1	1	1	1	1	1	1	1	1	1
Pollachius virens (pollock or saithe)															
Faroe	PV70	NEA	32	0	1	0	0	0	1	0	0	0	1	0	0
ICES VI	PV71	NEA	30	1	1	1	1	0	0	0	0	1	1	1	1
Iceland	PV72	NEA	32	1	1	1	1	0	0	0	0	0	0	1	0
NAFO 4VWX5	PV73	NWA	10	0	0	1	1	0	0	1	1	0	0	1	1
Northeast Arctic	PV74	NEA	32	1	0	0	0	0	1	1	0	1	0	0	0
North Sea	PV75	NEA	33	0	1	1	0	0	1	1	0	0	1	1	0
Theragra chalcogramma (walleye pollock)															
East Bering Sea	TC76	NEP	24	0	0	0	0	0	1	0	0	0	0	0	0
East Kamchatka	TC77	NWP	12	0	0	0	0	0	0	0	1	0	0	0	0
Gulf of Alaska, Alaska	TC78	NEP	25	0	1	0	0	0	0	1	0	0	1	0	0
Japan – Pacific coast of Hokkaido	TC79	NWP	15	0	1	0	0	0	1	0	0	0	1	0	0
West Bering Sea	TC80	NWP	21	0	1	0	0	0	0	0	0	0	0	0	0
Trisopterus esmarkii (Norway pout)															
North Sea	TE81	NEA	20	1	1	1	1	1	1	1	1	0	1	1	1
Urophycis chuss (red hake)															
NAFO Gulf of Maine, N. Georges Bank	UC82	NWA	13	1	0	1	1	1	0	0	0	1	0	0	1
NAFO Southern New England	UC83	NWA	15	0	0	0	0	0	0	0	0	0	0	0	0
Urophycis tenuis (white hake)															
NAFO 4T	UT84	NWA	14	0	0	0	0	0	0	0	0	0	0	0	0
Total (including *Gadus morhua*)				23	44	30	22	21	48	28	21	17	40	31	24
Proportion				0.27	0.52	0.36	0.26	0.25	0.57	0.33	0.25	0.20	0.48	0.37	0.29

Note: The stocks generally follow the Northwest Atlantic Fisheries Organization (NAFO) or the International Council for the Exploitation of the Sea (ICES) or the commonly used name based on their distribution. N, L, G, and P represent normal, lognormal, gamma, and Poisson distribution, respectively. Zero (0) and one (1) indicate unacceptable and acceptable model error distributions, respectively. The fishery distribution areas are classified as Northeast Atlantic (NEA), Northwest Atlantic (NWA), Northeast Pacific (NEP), Northwest Pacific (NWP), Southeast Atlantic (SEA), Southwest Atlantic (SWA), and Southwest Pacific (SWP) according to their geographic distribution.

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Fig. 5. A cluster analysis of distributions in stock–recruitment modeling for the *Gadus morhua* stocks.

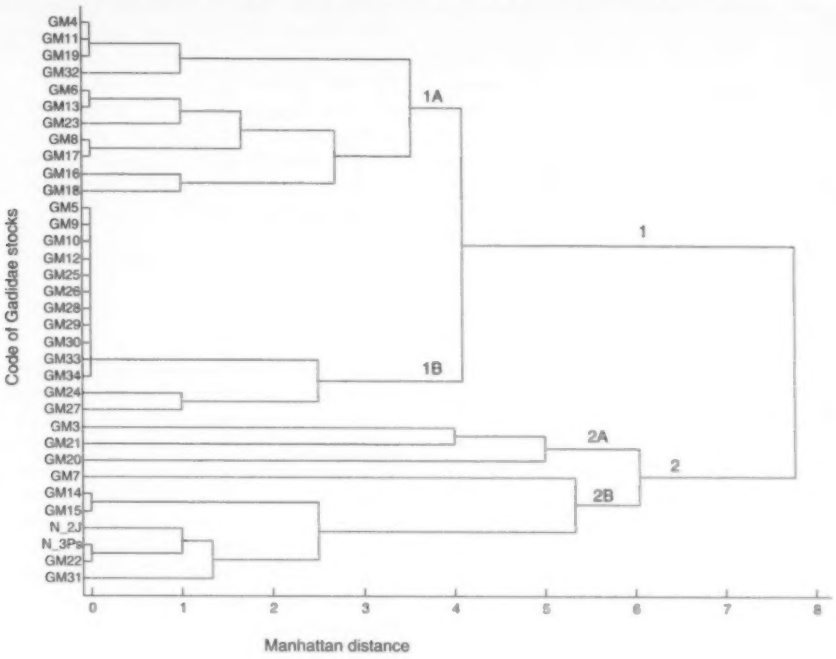

Table 4. Proportion of the stocks for which a particular model error distribution was identified as acceptable in the generalized linear model (GzLM).

	Cushing model				Ricker model				Beverton–Holt model				
Sample size	N	L	G	P	N	L	G	P	N	L	G	P	Total
$n \leq 15$	0.25	0.33	0.25	0.29	0.25	0.46	0.33	0.33	0.17	0.33	0.33	0.29	3.63
$15 < n \leq 30$	0.28	0.66	0.44	0.22	0.28	0.66	0.44	0.19	0.22	0.63	0.41	0.25	4.66
$n > 30$	0.27	0.50	0.33	0.27	0.20	0.53	0.20	0.23	0.20	0.40	0.33	0.30	3.77

Note: The calculation was done for different groups of stocks with different numbers of stock–recruitment observations (n). For a given stock, because multiple error distributions could be defined as acceptable, the sum of the proportions within a group of stocks may be larger than 1. N, L, G, and P represent normal, lognormal, gamma, and Poisson distribution, respectively.

Table 5. Proportion of the stocks for which a particular model error distribution was identified as acceptable in the generalized linear model (GzLM).

		Cushing model				Ricker model				Beverton–Holt model				
Geographic area	No. of stocks	N	L	G	P	N	L	G	P	N	L	G	P	Total
Northwest Atlantic	28	0.29	0.29	0.36	0.32	0.29	0.39	0.36	0.29	0.21	0.21	0.39	0.36	3.75
Northeast Atlantic	42	0.29	0.64	0.40	0.24	0.24	0.71	0.33	0.19	0.21	0.62	0.41	0.29	4.57
North Pacific	8	0.00	0.63	0.13	0.00	0.00	0.38	0.25	0.25	0.00	0.50	0.13	0.00	2.25
Southeast Atlantic	6	0.33	0.33	0.17	0.33	0.33	0.33	0.17	0.33	0.17	0.33	0.17	0.17	3.17

Note: The calculation was done for different groups of stocks distributed at different geographic ocean areas. For a given stock, because multiple error distributions could be defined as acceptable, the sum of the proportions within a group of stocks may be larger than 1. N, L, G, and P represent normal, lognormal, gamma, and Poisson distribution, respectively.

model error distributions has no obvious relationship with the sample size.

The proportion of the stocks for which the four distributions were identified as the acceptable model error structure in the GzLM differed somewhat between the stocks in the Northwest Atlantic area and those in the Northeast Atlantic area (Table 5). The lognormal distribution still has the highest probability of being defined as an acceptable model error structure in the *S–R* data of the stocks in the Northeast Atlantic. In the Northwest Atlantic, the gamma distribution has the highest probability of being defined as an acceptable model error structure in the stocks. The proportion of the four distributions identified as the acceptable *S–R* model error distribution differed less for Northwest Atlantic stocks than for Northeast Atlantic stocks. For stocks from the North Pacific areas, the lognormal distribution also had the highest

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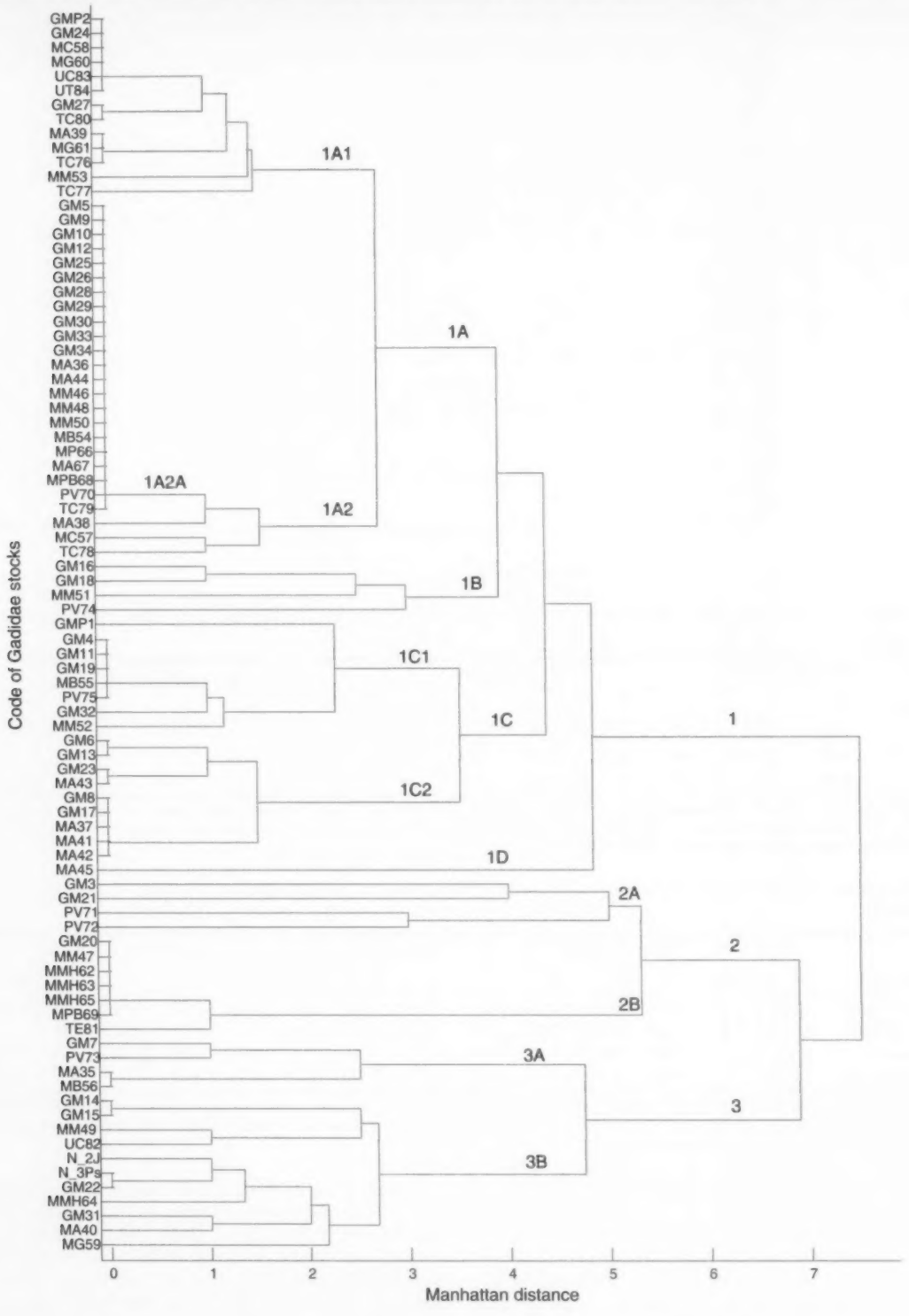
Fig. 6. A cluster analysis of distributions in stock–recruitment modeling for the Gadidae species and stocks.



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probability of being defined as an acceptable model error structure. For stocks from the Southeast Atlantic, each of the four error distributions defined as acceptable model error structures did not differ greatly (Table 5). Because this study only included eight stocks from the North Pacific and six stocks from the Southeast Atlantic and the sample sizes in those stocks are small, this result might not be conclusive. This study also included two stocks (MMH65 and MA67) from the Southwest Atlantic and Southwest Pacific ocean areas, respectively. However, because of their small number of stocks, we would not try to make a conclusion about their possible error distributions in modeling *S–R* data.

Discussion

An inappropriate model error assumption in *S–R* modeling was likely to yield an inappropriate estimation of *S–R* model parameters (Jiao et al. 2004). It is thus important to determine if the error structure assumed in the modeling is acceptable for a given *S–R* model and data set and to identify the most appropriate model error assumption for the *S–R* modeling. The normal error distribution tends to be sensitive to outliers in *S–R* models (Jiao et al. 2004). Large variations in environmental conditions may lead to skewed distributions of the recruitment, and even when both stock and recruitment follow a normal distribution, errors in modeling *S–R* data may not be normal. Thus the GzLM can improve the parameter estimation in the *S–R* modeling compared with the GLM, which is limited to the normal error distribution only.

This study suggests that the acceptable model error structures differ among data sets. It could differ among *S–R* models also, though 57% of the *S–R* data sets had the same acceptable model error structure in the three *S–R* models in this study. Error distributions assumed in the *S–R* modeling acceptable to one data set or model were not necessarily acceptable to other data sets (with the same model) or to other *S–R* models (with the same data set). Thus, the choice of error distributions should be fisheries- and model-specific. This study indicates that there are situations in which several distributions are acceptable and in which the GzLM could not determine which one was the most appropriate. This study also suggests that normal error distribution, although not usually used in *S–R* modeling now, may be an acceptable error structure in many cases.

The possibility of having several acceptable model error distributions or no acceptable model error distribution demonstrates the difficulty of selecting the best model error assumption for the parameter estimation in the *S–R* modeling. A quantitative goodness-of-fit criterion needs to be developed for identifying the most appropriate model error distribution when estimating parameters using the maximum likelihood method. The commonly used quantitative goodness-of-fit criteria, such as the maximum likelihood value and scaled variance, are only used for comparing the differences when the same model error distribution is used because the maximum likelihood function differs for different error structures assumed in *S–R* modeling.

The proportion of the stocks for which the particular model error distributions were identified as acceptable model error distributions in the GzLM analysis of *S–R* data in gadoid stocks implies that in modeling gadoid *S–R* data, the Beverton–Holt model is more sensitive to model error distribution assumption than the Cushing and Ricker models. The lognormal and gamma distributions have a higher probability of being defined as acceptable model error distributions, whereas the normal and Poisson distributions have a relatively lower probability of being defined as acceptable model error distributions. The results presented here might help select an acceptable model for stocks included in this study. However, we recommend reanalyzing the *S–R* data using the GzLM approach proposed in this study if more recent years of data are included in future studies, because the identification of acceptable error distributions tends to be data-specific.

The cluster analysis of *S–R* modeling error distributions suggests that there were no clear patterns in the identification of the acceptable model error distributions for stocks from different geographic areas and for different species. This variation in modeling error distribution is likely to result from intrinsic as well as extrinsic biological and physical processes (Armstrong and Shelton 1988; Fogarty 1993; Iles and Beverton 1998). Species or stocks in a local ecosystem can be influenced by large-scale climate changes, but the magnitude of the impacts might be different in ocean basins because of their distinctive oceanographic characteristics. That might explain the stock-specific *S–R* patterns and model error structures.

Four model error distributions were considered in this study. There are, however, other distributions, e.g., the Weibull distribution. GzLM can do parameter estimates only when model error distributions belong to the exponential family. For distributions that do not belong to the exponential family, the maximum likelihood method may be used to do parameter estimation and to perform model error distribution diagnostics. When identifying an acceptable model error structure, we recommend exploring the other possible model error structures for model error distributions not in the exponential family and not being limited to the four distributions shown in this study.

The choice of acceptable model error distributions can also be influenced by the choice of *S–R* models. Thus for stocks for which we could not identify an acceptable error distribution, the lack of an acceptable model error distribution might result from an inappropriate choice of *S–R* functions. Although we did not consider the choice of *S–R* functions in this study, we recommend that multiple choices of *S–R* functions be considered when no apparently acceptable or multiple acceptable error distributions can be defined, or when a certain *S–R* model does not fit the model well. For example, for cod (*Gadus morhua*) in NAFO 3Ps stock, the residual diagnostic plot showed that all four error distributions were acceptable when all three *S–R* models were used. The recruitment obviously could not be explained well by the stock biomass. A new *S–R* function needs to be developed considering biological and physical processes of recruitment in this case (Koster et al. 2001). Incorporation of vital environmental variables in *S–R* modeling may be necessary (Hilborn and Walters 1992).

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Instructions to Authors

Canadian Journal of Fisheries and Aquatic Sciences

The Journal welcomes manuscripts reporting significant new knowledge and understanding of fisheries and aquatic sciences. Manuscripts may concern cells, organisms, populations, communities, ecosystems, or processes that affect aquatic systems. They may cover a range of disciplines including biology and ecology of marine and freshwater organisms, limnology, oceanography, physiology, toxicology, genetics, economics, disease, and management. Manuscripts are selected for publication according to the extent and significance of new knowledge or ideas presented. Preference will be given to manuscripts that emphasize understanding of observed phenomena and interpretation of experimental results.

We encourage papers that lead from clearly stated purpose or rationale, and from testable hypotheses, concepts, or questions, to identifiable conclusions or syntheses. Such papers may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of aquatic sciences. **Rationale for the study and interpretation of the results should be set in a broad disciplinary or interdisciplinary context**. Methodological and modeling papers should include applications and provide verification of enhanced performance.

We continue to discourage papers that are essentially descriptive, except in emerging disciplines; have only site-specific or local applications (a certain year, place, taxon, chemical compound, etc.); confirm only previously established principles; or apply standard techniques without breaking new methodological ground. Studies that are clearly preliminary or fragmentary, or whose relevance to broader issues is not demonstrated, and interpretations solely of an unsupported speculative nature will not be entertained.

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Alternatively, submit manuscripts **in triplicate** to the Senior Editor, *Canadian Journal of Fisheries and Aquatic Sciences*, University of Guelph, Department of Zoology, Building #006, Room 107, Guelph, ON N1G 2W1, Canada. Enclose the manuscript text, tables, and figures on diskette, specifying the software package(s) and version(s) used; Microsoft Word is the preferred word-processing package for **review purposes**. **Packaging of manuscripts and illustrations should be robust enough to resist damage in transit.**

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Each manuscript is normally submitted to two referees for appraisal. However, the Senior Editor will return unreviewed those manuscripts that do not fall within the Journal's scope or character, and those that exceed the Journal's guidelines for prior publication as "extended abstracts" (guidelines available from the Editorial Office's Web site). Papers submitted for inclusion in Journal supplements are treated with the same rigor of review as articles in regular issues.

Responses to referees and revisions to manuscripts should normally be completed within 90 days. Manuscripts not returned within 90 days of receipt may be treated as new submissions unless the authors contact the Editorial Office.

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Preparation of manuscripts

General guidelines

Movement of manuscripts through review channels and the Editorial Office is greatly expedited if manuscripts are prepared in Journal style and format. General guidelines follow.

Type the manuscript on white paper (21.6 × 27.9 cm (8.5 × 11 in.)) on only one side of the page. Leave all margins at least 2.5 cm (1 in.) wide. Type only the title, authors' names and affiliations, and related footnotes on the first page. Number all pages beginning with the title page, including those for tables and captions for illustrations. **Double-space all parts of the manuscript**, including tables, captions for tables and figures, footnotes, and the reference list. Use italic font only for material that is to be set in italics. Do not use all capitals anywhere in the manuscript. Use the name-and-year system for literature citations.

Editorial practices

Spelling should follow that of *Webster's Third New International Dictionary* or the *Oxford English Dictionary*. Authors are responsible for consistency in spelling.

The *CBE Manual for Authors, Editors, and Publishers: Scientific Style and Format* (6th ed., 1994) published by the Council of Biology Editors, Inc., Chicago, IL 60603, U.S.A., is used as the authority in matters of form. Titles of periodicals are abbreviated as in *BIOSIS® Serial Sources* (BIOSIS, 2100 Arch Street, Philadelphia, PA 19103-1399, U.S.A.). Authors are responsible for ensuring the accuracy and completeness of their reference list. The Journal follows the names and spelling for fishes recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (5th ed., 1991, Spec. Publ. No. 20, American Fisheries Society) and the gene nomenclature for protein-coding loci outlined in Shaklee et al. (1990, Trans. Am. Fish. Soc. **119**: 2–15). **SI** units (Système international d'unités) should be used or SI equivalents should be given. This system is explained and other useful information is given in the *Metric Practice Guide* (2000) published by CSA International (178 Rexdale Blvd., Toronto, ON M9W 1R3, Canada). For practical reasons, some exceptions to SI units are allowed (noted in the editorial in the Journal, Vol. 40, No. 12).

Checklist for manuscripts

Attention to the following questions will expedite appraisal of manuscripts by referees and editors.

Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed and organized to facilitate comparison? Are there inconsistencies between tables and figures and the text, or within the text? Should some of the data be made available separately in a data or manuscript report or at a data depository?

If statistical analysis is included, is it subordinate to the research? When probability statements are made, are only the statistical tests cited and unnecessary statistical tables excluded?

Would any of the text be clearer if condensed? Are summary statements given at the beginning of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the **title** encompass the content of the report? Does the **Abstract** give the essentials of the new knowledge? Is the **Introduction** largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem? Are details of **Materials and methods** limited to what readers need to understand the design of the study and to judge the adequacy of the data? Are generalizations from the **Results** supported by the data provided? Are findings distinguished from inferences? Is the **Discussion** limited to interpretation and significance of the findings?

The most common technical problems in submitted manuscripts are listed below. Authors can hasten the processing of their papers if they pay attention to these points during manuscript preparation.

(1) Limit the abstract to one paragraph of about 175 words.
(2) Double-space all elements of the manuscript, including references, table captions, and figure legends.
(3) Avoid exclusive use of capitals anywhere in the manuscript, including headings, table captions, and figure legends.
(4) Italicize only Latin names of organisms and appropriate statistical and mathematical notations.
(5) Use correct SI symbols for units or measure in figures,

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tables, and text. Place a zero before the decimal for numbers less than unity.

(6) Avoid ambiguous forms such as g C/m^2/day; use g C·m^{-2}·day^{-1}.

(7) Identify the test used to test statistical significance and give the probability value. No reference is needed for common statistical tests.

(8) In the text, generalize from tables and figures; avoid repeating all of the details. Be sure each table and figure can stand on its own and is referred to in the text in numerical order. The captions should explain the purpose of the table or figure.

(9) Include an acknowledgement section at manuscript stage, not when page proofs arrive.

(10) Provide the person's initials and mailing address when referring to personal communications.

(11) Delete unnecessary references that do not apply directly to the problem.

(12) Check references carefully against text citations and vice versa to ensure exact correspondence. Provide an availability statement for less easily retrieved material, e.g., available from Department of Economics, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.

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Parts of the manuscript

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Organize the manuscript on the basis of the purpose or scope of the study as stated in the introduction. Ensure that the title and headings are in harmony with the statement of purpose.

Before writing any of the manuscript, list tentative headings in as few ranks as possible. Rework them until they appear to allow logical development for the reader; usually, chronological order is not effective. The findings will be more readily appreciated if methods, findings, and discussion are given in separate sections.

Organize tables and figures to facilitate comparisons, grouping related data in as few tables and figures as feasible. As far as possible, make the tables and figures clear without reference to the text.

Begin sections and paragraphs with topic sentences containing generalizations that lead readily to the particulars. Giving a conclusion first and then supporting it not only improves readability but also facilitates assessment by other scientists. Failure to give the most newsworthy generalizations first is one of the most prominent shortcomings in presentation of manuscripts.

Make certain that everything in each section is relevant to the heading and that everything in each paragraph is relevant to the topic (opening) sentence.

Before writing any paragraphs, try writing the topic sentences for all of them and arranging these in appropriate order.

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Limit the title to what is documented in the manuscript. It is the key to the article and should clearly and concisely reveal what appears in the paper itself. The title serves two functions: (1) it allows the reader to judge whether or not the article is of potential interest and (2) it should provide enough information to permit the reader to judge the scope and potential importance of the article. Words in the title should convey a maximal amount of information and identify the nature of the research, organism used, and where appropriate, the technical approach (e.g., X ray, chromatography, mathematical analysis). Titles should not begin with a numeral or introductory prepositions such as "On" or "Towards" or expressions such as "A contribution to..." or "Investigations on...". Good titles greatly assist scientists and librarians in using scientific literature and aid indexers in preparing titles for keyword indexes. Series titles should be avoided.

Abstract

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Like the title, the abstract enables readers to determine the paper's content and decide whether or not they need to read the entire article. Begin the abstract with the main conclusion from the study, and support it with the relevant findings. Limit details of methods to those needed in understanding what was done, and work them into statements of findings. Avoid using phrases such as "...is discussed" or "...was found"; be specific. As the abstract is often divorced from the main body of the paper by abstracting and indexing services and is the only part of a paper some readers ever see, it is important that it accurately reflect the paper's contents and be completely self-contained (i.e., any *essential* references) in a retrievable form (e.g., R.B. Deriso. 1980. Can. J. Fish. Aquat. Sci. **37**: 268–282).

Introduction

Limit the introduction largely to the scope, purpose, and rationale of the study. Restrict the literature review and other background information to that needed in defining the problem or setting the work in perspective. Try beginning with the purpose or scope of the work, defining the problem next, and adding guideposts to orient the reader. An introduction generally need not exceed 375–500 words.

Materials and methods

Materials and methods provides the framework for getting answers to the questions posed in the purpose of the work.

Limit the information on materials and methods to what is needed in judging whether the findings are valid. To facilitate assessment, give all of the information in one section when possible. Refer to the literature concerning descriptions of equipment or techniques already published, detailing only adaptations. Often, it helps to begin statements on procedures with a phrase indicating the purpose, such as "To determine...we...". If the section is long, consider using subheadings corresponding to headings for the findings.

Results

Limit the results to answers to the questions posed in the purpose of the work, and condense them as comprehensively as possible. Give the findings as nearly as possible in the terms in which the observations or measurements were made so as to avoid confusion between facts and inferences. State noteworthy findings to be noted in each table and figure, and avoid restating in the text what is clear from the captions. Material supplementary to the text can be archived in

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Discussion

Limit the discussion to giving the main contributions of the study and interpreting particular findings, comparing them with those of other workers. Emphasis should be maintained on synthesis and interpretation and exposition of broadly applicable generalizations and principles. If these are exceptions or unsettled points, note them and show how the findings agree or contrast with previously published work. Limit speculation to what can be supported with reasonable evidence. End the discussion with a short summary of the significance of the work and conclusions drawn. If the discussion is brief and straightforward, it can be combined with the results section.

Acknowledgements

We strongly urge authors to limit acknowledgments to those who contributed substantially to scientific and technical aspects of the paper, gave financial support, or improved the quality of the presentation. Avoid acknowledging those whose contribution was clerical only.

References

References should be selected judiciously and be largely restricted to significant, published literature. References to unpublished data, manuscripts in preparation or submitted to other journals, progress reports, and unpublished papers given at annual meetings may not be cited in the reference list but may be noted in the text as unpublished data or personal communications (include mailing addresses). If consultants' reports or other documents of limited circulation must be cited, they should carry with them an availability statement explaining where the document can be obtained. **Citations of literature in the text should be carefully checked against those in the reference list and vice versa to ensure exact correspondence.** Nearly every manuscript submitted to the Journal contains errors in the references.

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Footnotes to material in the text should not be used unless they are unavoidable, but their use is encouraged in tables. Where used in the text, footnotes should be cited in the manuscript by superscript Arabic numbers (except in the tables, see below) and should be numbered serially beginning with any that appear on the title page. Each footnote should be typed on the manuscript page on which the reference to it is made; **footnotes should not be included in the list of references**.

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Equations should be clearly typed; triple-spacing should be used if superscripts and (or) subscripts are involved. Superscripts and subscripts should be legible and carefully placed. Distinguish between lowercase *l* and the numeral *one*, and between capital *O* and the numeral *zero*. A letter or symbol should represent only one entity and be used consistently throughout the paper. Each variable must be defined in the text or in a **List of symbols** to appear after the reference list. Variables representing vectors, matrices, vector matrices, and tensors must be clearly identified. Numbers identifying equations must be in parentheses and placed flush with the **left margin**. In numbering, no distinction is made between mathematical and chemical equations.

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Appendices should be indicated sequentially by A, B, C, etc., and figures and tables in the appendices should be numbered separately from those used in the main body of the paper, for example, Fig. A1, Table A1, etc.

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Abbreviate terms denoting units of weight and measurement in the text only when they are preceded by numerals.

becquerel (Bq)
calorie (cal)
centimetre (cm)
centimetre, square (cm^2)
centimetre, cubic (cm^3)
centimetres per gram per second ($cm \cdot g^{-1} \cdot s^{-1}$)
coulomb (C)
decimetre (dm)
degree Celcius (°C)
degrees of freedom (df)
gram (g)
hectare (ha)
hertz (Hz)
hour (h)
joule (J)
kilometre (km)
litre (L)
lumen (lm)
lux (lx)
metre (m)
metre, square (m^2)
metre, cubic (m^3)
micrometre (μm)
milligram (mg)
millilitre (mL)
millimetre (mm)
millimetre, square (mm^2)
minute (min)
molar mass (M)
mole (mol)

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moles per litre (mol/L, M)
Pascal (Pa)
second (s)
standard deviation (SD)
standard error (SE)
tonne (metric ton) (t)
volt (V)
volume (vol)
watt (W)

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Reference lists

References should be listed at the end of the paper in alphabetical order according to surnames of the first author. References with the same first author are listed in the following order. (1) Papers with **one author only** are listed first in chronological order, beginning with the earliest paper. (2) Papers with **dual authorship** follow and are listed in alphabetical order by the last name of the second author. (3) Papers with **three or more authors** appear after the dual-authored papers and are arranged chronologically.

The following bibliographic citations illustrate the punctuation, style, and abbreviations (according to *CASSI* or *BIOSIS® Serial Sources*) for references.

Journal article

Peterman, R.M. 1982. Model of salmon age structure and its use in preseason forecasting and studies of marine survival. Can. J. Fish. Aquat. Sci. **39**: 1444–1452.

Entire issue of journal

Gordon, D.C., Jr., and Hourston, A.S. (*Editors*). 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. **40**(Suppl. 1).

Book in a series

Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. No. 184.

Book not in a series

LeBlond, P.H., and Mysak, L.A. 1978. Waves in the ocean. Elsevier, New York.

Part of book

Healey, M.C. 1980. The ecology of juvenile salmon in Georgia Strait, Britsh Columbia. *In* Salmonid ecosystems of the North Pacific. *Edited by* W.J. Neil and D.C. Himsworth. Oregon State University Press, Corvallis, Oreg. pp. 203–229.

Corporate author

American Public Health Association, American Water Works Association, and Water Pollution Control Federation. 1975. Standard methods for the examination of water and wastewater. 14th ed. Washington, D.C.

Theses

Kutty, M.N. 1999. Some studies on the respiratory quotient in goldfish and rainbow trout. Ph.D. thesis, University of Toronto, Toronto, Ont. Natl. Libr. Can., Can. Theses Microfilm No. 646.

Reports

Smith, J.E. 1981. Catch and efforts statistics of the Canadian groundfish fishery on the Pacific coast in 1980. Can. Tech. Rep. Fish. Aquat. Sci. No. 1032.

Translation

Koike, A., and Ogura, B. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. **64**: 1–11. [Translated from Japanese by Can. Transl. Fish. Aquat. Sci. 4950, 1983.]

Word list

The spelling of the following words is frequently inconsistent in submitted manuscripts. We prefer that authors adhere to the Journal's house style for these commonly used terms:

age class (n.)
aquaculture (n.)
Arctic char (n.)
brackish water (n.)
brackish-water (adj.)
cold water (n.)
cold-water (adj.)
deep sea (n.)
deep-sea (adj.)
deep water (n.)
deepwater (adj.)
fresh water (n.)
freshwater (adj.)
ground water (n.)
groundwater (adj.)
hard water (n.)
hardwater (adj.)
headwater (n., adj.)
lake water (n., adj.)
meltwater (n., adj.)
open water (n.)
open-water (adj.)
percent (n.)
salt water (n.)
salt-water (adj.)

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sea-run (adj.)
seawater (n., adj.)
shallow water (n.)
shallow-water (adj.)
size class (n.)
snowmelt (n.)
snowpack (n.)
soft water (n.)
softwater (adj.)
tidewater (n., adj.)
t test (n., adj.)
warm water (n.)
warm-water (adj.)
year class (n.)
young of the year (n.)
young-of-the-year (adj.)

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Recommandations aux auteurs

Journal canadien des sciences halieutiques et aquatiques

La Rédaction encourage la soumission d'articles contribuant à l'enrichissement des connaissances des sciences halieutiques et aquatiques. Les articles peuvent porter sur les cellules, les organismes, les populations, les communautés, les écosystèmes ou les procédés qui affectent les systèmes aquatiques. Ils peuvent traiter de disciplines variées y compris la biologie et l'écologie des organismes d'eau douce et d'eau salée, la limnologie, l'océanographie, la physiologie, la toxicologie, la génétique, l'économie, les maladies et la gestion. Les articles sont choisis selon la portée et l'importance des nouvelles connaissances ou idées qu'ils contiennent. On accorde la préséance aux articles qui contribuent à la compréhension de phénomènes observés et à l'interprétation de résultats expérimentaux.

Nous invitons les auteurs à soumettre des articles ayant des objectifs précis ou relevant des hypothèses, concepts ou questions vérifiables et se terminant par de solides conclusions ou d'utiles synthèses. Ces articles enrichissent, changent, mettent en question ou réorientent les connaissances acquises sur divers aspects des sciences aquatiques. **La raison d'être de l'analyse et l'interprétation des résultats doivent être situées dans un vaste contexte disciplinaire ou interdisciplinaire.** Les articles de méthodologie et de modélisation doivent inclure des applications et prouver la supériorité de la méthodologie ou du modèle explicité.

La Rédaction décourage la soumission d'articles simplement descriptifs (à moins qu'il ne s'agisse de nouvelles disciplines), d'application très limitée (applicable à une seule année, une seule région ou un seul taxon, portant sur un unique composé chimique, etc.); d'articles qui ne font que reprendre les principes énoncés dans des articles précédents; et d'articles rendant compte de l'application de normes sans gain de méthodologie. Les études préliminaires ou fragmentaires, ou dont la pertinence à grande échelle n'est pas démontrée, et les interprétations purement spéculatives sont carrément rejetées.

Les articles doivent être aussi complets que possible. S'il est impossible d'inclure toute les données pertinentes dans un seul article, l'auteur devra inclure des renvois à des articles connexes et soumettre ceux-ci avec son propre article.

Le Journal publie le genre de textes suivants :

Articles — Études de vaste portée qui constituent de nouvelles contributions à la science.

Perspectives — Synthèses, synthèses critiques ou réévaluations de concepts ou de paradigmes couramment admis.

Discussions — Commentaire ou réponse sur des sujets récemment abordés dans le Journal.

Communications rapides — Présentations de nouveaux concepts, descriptions de nouvelles méthodologies ou courts textes sur des sujets d'actualité ou controversés.

On peut obtenir les caractéristiques précises de chacun de ces genres sur le site Web du Bureau de la rédaction http://www.uoguelph.ca/~cjfas/.

Processus de publication

La Rédaction **encourage les auteurs à soumettre leurs manuscrits par courriel** à cjfas@uoguelph.ca en format Word, WordPerfect ou PDF. Pour obtenir de plus amples renseignements sur la soumission électronique, y compris les formats de fichier acceptés, communiquez directement avec la Rédaction.

Si vous **optez pour la soumission par courrier**, vous devez soumettre les manuscrits (**en triple**) à la directrice scientifique principale, *Journal canadien des sciences halieutiques et aquatiques*, University of Guelph, Département de zoologie, édifice 006, bureau 107, Guelph, ON N1G 2W1, Canada. Veuillez inclure le texte, les tableaux et les figures du manuscrit sur disquette, en précisant le(s) progiciel(s) et la (les) version(s) utilisés; le logiciel de traitement de textes préférés est Microsoft Word pour **l'examen par les réviseurs**. **Les manuscrits et les illustrations doivent être solidement emballés afin d'être protégés lors de l'expédition.**

Nous encourageons la soumission d'articles brefs, de style clair. Nous accepterons d'examiner les manuscrits plus longs si leur importance et leur interprétation de nouvelles connaissances en justifient la longueur.

Tous les manuscrits doivent être accompagnés d'une lettre qui fait état (1) des principaux points et de l'importance du travail, (2) de la participation de tous les auteurs au manuscrit et de leur approbation de ce dernier, (3) de l'assurance que le manuscrit en question n'est pas en cours d'examen aux fins de publication dans une autre revue, (4) de suggestions quant aux arbitres éventuels, (5) d'autres manuscrits, y compris de résumés détaillés, contenant une information identique ou similaire à celle contenue dans le manuscrit soumis et (6) des numéros de téléphone et de télécopieur ainsi que du courriel et de l'adresse de chaque auteur. L'auteur devra, de préférence, conserver les originaux du texte dactylographié et des figures (sauf les demi-teintes) jusqu'à ce qu'on les lui demande.

La directrice scientifique principale reconnaît la possibilité que des conflits d'intérêts réels ou perçus surviennent à la suite de circonstances intellectuelles, personnelles ou financières liées aux travaux de recherche. Or, les manuscrits devraient inclure une divulgation de toute source de financement de la recherche. De plus, la lettre de transmission devrait comprendre une explication de tout conflit d'intérêts, réel ou perçu, qui pourrait survenir lors du processus d'examen par les pairs. Si de tels conflits ne sont pas divulgués, le manuscrit pourrait être refusé.

Chaque article est habituellement soumis à une évaluation par au moins deux réviseurs. Toutefois, la directrice scientifique principale renverra sans les évaluer tout article qui ne re-

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flète pas la portée ou le caractère du Journal et les articles qui débordent des limites imposées pour la publication sous forme de « résumés approfondis ». On obtiendra les directives à cet égard sur le site Web du Bureau de la rédaction. Les articles soumis aux fins de publication dans un supplément sont soumis au même rigoureux exercice d'examen que les articles des numéros réguliers.

On demande habituellement aux auteurs d'examiner les commentaires des réviseurs et de modifier leur texte en conséquence en 90 jours, tout au plus. Faute de respecter ce délai, l'article renvoyé par l'auteur sera traité comme une nouvelle soumission à moins que l'auteur n'ait au préalable dûment communiqué avec le Bureau de la rédaction.

Droits de reproduction — Lorsqu'un article contient de la documentation (tableaux, figures, schémas, etc.) déjà publiée, il incombe à l'auteur d'obtenir **une permission écrite du titulaire de ces droits d'auteur** pour permettre la reproduction de l'information **en format imprimé et électronique**. La lettre d'autorisation doit accompagner le manuscrit soumis, sans quoi le processus de publication pourra être retardé. Cette lettre sera exigée avec toute mention du type « Tirée de... ». Si une illustration est modifiée, de sorte qu'une telle autorisation n'est pas requise, la formulation doit être explicite : « Modifiée d'après... ». Si l'illustration est reconstituée à partir d'informations tirées d'autres auteurs la mention doit être du même type que pour une référence.

Soumission de la version approuvée — Les auteurs sont priés de soumettre **une copie imprimée ainsi qu'une copie sur disquette de la version approuvée de l'article seulement**. Les fichiers de texte et les fichiers d'illustrations devront être soumis sur des disquettes distinctes. Le nom des auteurs doit être indiqué clairement sur chaque disquette soumise. Le **texte** (y compris les tableaux) devrait être soumis en format de traitement de texte (WordPerfect, Microsoft Word ou TeX est préférable, compatible à IBM ou Macintosh). Les macros en TeX et la documentation pour la préparation des soumissions sont maintenant disponibles à ftp://ftp.tex.ac.uk/tex-archive/macros/latex/contrib/nrc/, ftp://ftp.dante.de/tex-archive/macros/latex/contrib/nrc/ et ftp://ctan.tug.org/tex-archive/macros/latex/contrib/nrc/. Il importe d'indiquer le logiciel de traitement de texte utilisé, la version, de même que le type d'ordinateur (IBM ou Macintosh). En ce qui a trait aux **illustrations**, il convient de se reporter à la section « Préparation des fichiers électroniques des illustrations ». Tout article devra être accompagné d'une lettre faisant foi du fait que la version du texte sur disquette reflète exactement la version imprimée soumise.

Épreuves en placard — Une épreuve en placard, des épreuves des illustrations, une copie de l'article corrigé et un bon de commande de tirés à part sont envoyés à l'auteur correspondant. **Les épreuves en placard doivent être relues attentivement car elles ne sont pas corrigées par les Presses scientifiques du CNRC.** Elles doivent en outre être retournées dans les 48 h suivant leur réception. Au stade des épreuves, il n'est plus temps d'apporter des modifications importantes ni de faire des ajouts ou des suppressions. Les frais occasionnés par des modifications excessives devront être assumés par les auteurs.

Tirés à part — Pour obtenir des tirés à part, il est nécessaire de remplir le bon de commande à cet effet et de le retourner avec le paiement (chèque, numéro de carte de crédit, numéro du bon d'achat ou pièce de journal interne) en même temps que les épreuves et l'article corrigés. Le tarif des tirés à part commandés après la parution du numéro du Journal est fortement majoré. **Le Journal n'offre pas de tirés à part gratuits; ceux-ci ne sont postés qu'après réception d'un numéro du bon d'achat ou du paiement.**

Transfert des droits d'auteur — Tous les auteurs doivent compléter un formulaire de transfert des droits d'auteur au CNRC. On obtiendra ces formulaires auprès de la directrice scientifique principale, dans le premier numéro de chaque volume ou sur le site Web des Presses scientifiques du CNRC.

Toute **permission de republication** partielle ou intégrale d'un article doit être obtenue auprès des Presses scientifiques du CNRC.

Préparation des manuscrits

Directives générales

Le processus de publication sera grandement facilité si les articles sont préparés conformément au style du Journal.

Dactylographiez le manuscrit sur papier blanc (21,6 sur 27,9 cm (8,5 sur 11 po)) sur un côté de la page. Laissez toujours une marge d'au moins 2,5 cm (1 po). Sur la première page, dactylographiez le titre, les noms et affiliations des auteurs et les renvois qui s'y rapportent. Numérotez toutes les pages, à commencer par la page-titre, de même que celles contenant les tableaux et les légendes des illustrations. Tout le manuscrit, y compris tableaux, légendes des tableaux et des figures, renvois et liste de références, doit être dactylographié à **double interligne**. N'utiliser l'italique que pour les passages qui doivent paraître en italique dans le document final. En aucun endroit du manuscrit n'écrivez entièrement en majuscules. Pour les références citées dans le texte, utilisez le système nom et année,

Dispositions générales

L'orthographe doit suivre *Le Grand Robert*. Les accents doivent être insérés sur les majuscules. Les auteurs sont responsables de l'uniformité de l'orthographe.

Le *CBE Manual for Authors, Editors, and Publishers : Scientific Style and Format* (6e éd., 1994, Council of Biology Editors, Inc., Chicago, IL 60603, É.-U.) sert de guide quant à la forme de la présentation. Les titres de périodiques sont abrégés suivant *BIOSIS® Serial Sources* (BIOSIS, 2100 rue Arch, Philadelphia, PA 19103-1399, É.-U.). C'est la responsabilité des auteurs de s'assurer que leurs références sont complètes et exactes. Pour les noms de poissons et leur orthographe, le Journal suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (5e éd., 1991, Spec. Publ. No. 20, American Fisheries Society). Pour la nomenclature génétique pour les locus de codage des protéines, le Journal suit les recommandations contenues dans Shaklee et al. (1990, Trans. Am. Fish. Soc. **119** : 2–15). Il est recommandé de se servir du **Système international d'unités** ou, tout au moins, de fournir les équivalences en unités SI. Ce système est décrit dans le *Guide de familiarisation au système métrique*, publié en 2002 par l'Association canadienne de normalisation (5060 Spectrum Way, bureau 100, Mississauga, ON L4W 5N6, Canada). Pour des raisons pratiques, on permet certaines exceptions à l'utilisation du Système international d'unités (comme dans un éditorial du Journal, vol. 40, no 12).

Liste de contrôle pour manuscrits

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les rédacteurs.

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes aux buts de l'étude?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou à l'intérieur du texte? Est-ce que certaines données devraient être présentées

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séparément dans un rapport manuscrit ou dans un dépôt de données?

Si une analyse statistique est effectuée, la statistique cède-t-elle le pas à la recherche? Dans des énoncés de probabilité, les tableaux statistiques inutiles sont-ils exclus et seulement les tests statistiques cités?

Le texte gagnerait-il en clarté s'il était plus condensé, en tout ou en partie? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphes sont-ils pertinents au sujet traité? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction?

Le **titre** est-il représentatif du contenu du rapport? Le **Résumé** donne-t-il l'essentiel des connaissances nouvelles? L'**Introduction** se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude? La revue de la littérature se limite-t-elle à la définition du problème? La section **Matériel et méthodes** contient-elle le minimum de détails qui permettront aux lecteurs de saisir les grandes lignes de l'étude et de juger de la valeur des données? Les généralisations sur les **Résultats** sont-elles adéquates? Permettent-elles de distinguer entre constatations et déductions? La **Discussion** est-elle limitée à l'interprétation et à l'évaluation des découvertes?

Sont énumérés, ci-dessous, des façons d'éviter les problèmes techniques les plus communs dans la soumission des manuscrits. En accordant une attention particulière à ces points lors de la préparation de leurs manuscrits, les auteurs peuvent accélérer le traitement des articles.

(1) Limiter le résumé à un paragraphe d'environ 175 mots.
(2) Dactylographier à double interligne tous les éléments du manuscrit, y compris la bibliographie et les légendes des tableaux et des figures.
(3) Éviter partout l'emploi exclusif de majuscules, y compris dans les en-têtes et les légendes des tableaux et des figures.
(4) Ne composer en italique que les noms latins d'organismes et certaines notations statistiques et mathématiques qui devront être imprimés en italique.
(5) Dans les figures, les tableaux et le texte, exprimer les unités de mesure par leurs symboles SI propres. Pour les nombres inférieurs à l'unité, placer un zéro avant la virgule décimale.
(6) Éviter les formes ambiguës, telles que g C/m^2/jour; utiliser plutôt g C·m^{-2}·jour^{-1}.
(7) Identifier le test qui a servi à évaluer la signification statistique, donnant également la valeur de probabilité. S'il s'agit de tests communs, il n'est pas nécessaire d'en donner la référence.
(8) Dans le texte, généraliser à partir des tableaux et des figures; éviter une répétition de tous les détails. S'assurer que tous les tableaux et figures sont indépendants et mentionnés dans le texte dans l'ordre numérique. Les légendes doivent indiquer le but du tableau ou de la figure.
(9) Préparer la section des remerciements au stade du manuscrit et non à celui des épreuves.
(10) En référant à des communications personnelles, donner les initiales et l'adresse postale de la personne en cause.
(11) Éliminer toutes références qui ne s'appliquent pas directement au problème.
(12) Vérifier soigneusement la correspondance des références en regard des citations dans le texte et vice versa. Dans le cas de matériel difficilement accessible, indiquer l'endroit où le trouver (p. ex., disponible auprès du Département de biologie, Université Laval, Sainte-Foy, QC G1K 7P4, Canada).
(13) Éliminer les virgules entre le nom et la date dans les citations telles que (Smith 1990) et ne pas souligner ni mettre en italique « et al. ».
(14) Aux fins de la révision, les photocopies des figures, sauf pour les demi-teintes, sont appropriées. Sur demande, lorsqu'il s'agira de publier l'article, envoyer des photographies, des imprimés laser ou les dessins originaux/fichiers électroniques des figures (voir « Illustrations » et « Préparation des fichiers électroniques des illustrations »). Utiliser autant que possible un lettrage uniforme.

Parties du manuscrit

Organisation

Organiser le manuscrit par rapport au but ou à la portée de l'étude, tels qu'énoncés dans l'introduction. Il est particulièrement important que le titre et les sous-titres soient en harmonie avec les objectifs.

Avant de commencer la rédaction du manuscrit, dresser une liste provisoire des sous-titres ou en-têtes, avec le moins de divisions possible. Retoucher les jusqu'à ce qu'ils semblent assurer, pour le lecteur, une marche logique; ordinairement, l'ordre chronologique ne sera pas satisfaisant. Il sera plus facile d'évaluer les résultats si méthodes, résultats et discussion sont décrits dans des sections séparées.

Organiser les tableaux et les figures de façon à faciliter les comparaisons, groupant les données apparentées en aussi peu de tableaux et de figures que possible. S'assurer que ces derniers sont aussi clairs que possible sans référence au texte.

Commencer les sections et les paragraphes par des énoncés généraux qui aboutissent naturellement à des énoncés particuliers. Si la conclusion est donnée d'abord puis appuyée ensuite, non seulement le travail sera plus facile à lire, mais aussi les autres scientifiques pourront plus aisément en évaluer les résultats. Dans la rédaction des manuscrits, le défaut le plus commun est d'omettre de donner, au début, les généralités les plus dignes de mention.

Voir à ce que le matériel de chaque section soit pertinent à l'en-tête et que le matériel de chaque paragraphe se rapporte à la première phrase introduisant le sujet.

Avant de rédiger les paragraphes, composer la phrase thème de chaque paragraphe et disposer ces phrases dans l'ordre approprié.

Titre

Limiter le titre à ce que l'étude veut démontrer. C'est la clé de l'article et il devrait refléter clairement et brièvement le contenu de l'étude. Le titre a deux fonctions : (1) il permet au lecteur de juger si, oui ou non, l'article peut avoir un intérêt et (2) il devrait fournir suffisamment d'information pour permettre au lecteur de juger de la portée et de l'importance potentielle de l'article. Les mots du titre devraient fournir un maximum d'information et identifier la nature de la recherche, de l'organisme utilisé et, au besoin, la méthode d'approche technique (p. ex., rayons X, chromatographie, analyse mathématique). Les titres ne devraient pas commencer par un chiffre ou par des prépositions d'introduction telles que « Sur » ou « Vers », ou des expressions telles que « Contribution à… » ou « Recherche sur… ». De bons titres facilitent le classement des publications et leur utilisation par les scientifiques et les bibliothécaires. On évitera les titres en séries.

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Résumé

Un résumé doit accompagner chaque texte et exposer brièvement, en 175 mots ou moins, ce qui a été fait, ce qui a été découvert et les conclusions auxquelles on est arrivé. Les auteurs qui peuvent soumettre des résumés dans les deux langues officielles du Canada, c'est-à-dire en français et en anglais courants, sont encouragés à le faire.

Comme le titre, le résumé permet aux lecteurs de prendre connaissance du contenu de l'article et de décider si, oui ou non, il leur faut lire ce dernier en entier. Indiquer, au début du résumé, la principale conclusion de l'étude et l'appuyer par des découvertes pertinentes. Ne donner que les détails des méthodes nécessaires à la compréhension de ce qui a été fait et les insérer dans l'énoncé des découvertes. Éviter l'emploi de phrases telles que « ... on y analyse » ou « ... a été trouvé » ; être plus spécifique. Comme le résumé est souvent séparé du corps principal de l'article par les services d'analyse et de classement, c'est la seule partie d'un travail que certains lecteurs auront l'occasion de voir; il importe donc qu'il reflète précisément le contenu du travail et qu'il soit complet en lui-même (c.-à-d., les références absolument *essentielles* sont indiquées, sous forme retraçable, p. ex., R.B. Deriso. 1980. Can. J. Fish. Aquat. Sci. **37** : 268–282).

Introduction

Limiter l'introduction à la portée, au but et à la raison de l'étude. Ne mentionner que les travaux publiés et autres informations nécessaires à la définition du problème et à la perspective du travail. Commencer avec le but ou la portée du travail, définir ensuite le problème et ajouter ici et là des jalons qui aideront à orienter le lecteur. En général, une introduction n'a pas besoin de dépasser 375–500 mots.

Matériel et méthodes

Cette section renferme ce dont on a besoin pour trouver réponse aux questions soulevées dans les objectifs du travail.

Limiter les renseignements à ce qui est nécessaire pour juger de la validité des découvertes. Cette évaluation sera facilitée si toute l'information est présentée, autant que possible, dans une section. S'il s'agit d'outillage ou de techniques déjà publiés, référer aux publications et ne décrire en détail que les adaptations. Il y a souvent avantage à commencer un énoncé des méthodes par une phrase qui en indique le but, comme : « Afin de déterminer... nous... ». Si la section est longue, utiliser des sous-titres correspondant à ceux de la section des résultats.

Résultats

Limiter les résultats aux réponses apportées aux questions en rapport avec le but de l'étude; que ces réponses soient aussi complètes que possible, tout en étant concises. Exprimer, autant que possible, les découvertes dans les mêmes termes que les observations ou les mesures, évitant ainsi de confondre faits et spéculations. Dégager les généralités des tableaux et des figures et y référer en évitant de répéter dans le texte ce que les légendes devraient exprimer clairement. Le matériel complémentaire au texte peut être classé dans les séries de rapports ou dans un dépôt de données reconnu; et on y référera dans le texte.

Discussion

Limiter la discussion à l'énoncé de la principale contribution de l'étude et à l'interprétation de découvertes particulières, les comparant avec celles d'autres auteurs. On continuera à mettre l'accent sur la synthèse et l'interprétation, ainsi que sur l'exposition de généralisations et de principes largement applicables. S'il s'agit d'exceptions ou de points douteux, les noter et faire ressortir la manière dont les résultats corroborent ou contredisent les travaux déjà publiés. Limiter la spéculation à ce qui peut être appuyé sur des preuves raisonnables. Terminer cette section par un court résumé de l'importance du travail et des conclusions auxquelles il a conduit. Si la discussion est brève et précise, elle peut être combinée avec les résultats en une seule et même section.

Remerciements

Nous recommandons fortement aux auteurs de limiter les remerciements aux personnes qui ont contribué d'une manière substantielle aux aspects scientifiques et techniques de l'article, fourni une aide financière ou amélioré la qualité de la présentation. Éviter de mentionner les personnes qui n'ont fourni qu'un travail de soutien.

Bibliographie

On choisira les références avec soin, les limitant aux publications importantes. On ne peut citer dans cette section les références à des données inédites, manuscrits en préparation ou soumis à d'autres périodiques, états des travaux et communications inédites présentées à des réunions annuelles. On peut toutefois les mentionner dans le texte à titre de données inédites ou de communications personnelles (incluant les adresses). Si l'on doit citer des rapports d'experts-conseils ou d'autres documents dont la distribution est limitée, on devra préciser l'endroit où l'on peut se les procurer. **On doit s'assurer que les références mentionnées dans le texte correspondent à celles qui sont contenues dans la bibliographie et vice versa.** Presque tous les manuscrits soumis au Journal contiennent des erreurs dans cette section.

Notes infrapaginales

Les notes infrapaginales ne devraient figurer dans le texte que lorsqu'elles sont inévitables, mais leur utilisation dans les tableaux est encouragée. Lorsque les notes infrapaginales figurent dans le texte, leurs appels devraient être désignés par des chiffres arabes en exposant (sauf dans le cas des tableaux, voir ci-dessous) et numérotés consécutivement à partir de la première note infrapaginale, y compris toute note apparaissant en page titre. Chaque note doit figurer au bas de la page où elle est signalée, **pas dans la bibliographie**.

Équations

Les équations doivent être dactylographiées clairement, à triple interligne si elles incluent des exposants ou des indices. Les exposants et les indices doivent être lisibles et correctement placés. Il convient de faire une distinction entre la lettre *l* et le chiffre *un*, et entre la lettre majuscule *O* et le chiffre *zéro*. Une lettre ou un symbole ne devrait représenter qu'une seule entité et devrait être utilisé de façon uniforme dans l'article. Chaque variable doit être définie dans le texte ou dans une **liste des symboles** devant apparaître après la bibliographie. Les variables représentant des vecteurs, des matrices, des matrices vectorielles et des tenseurs doivent être clairement définies. Les numéros d'équation doivent être identifiés par des chiffres arabes placés entre parenthèses et alignés avec la **marge de gauche**. Aucune distinction n'est faite entre la numérotation des formules mathématiques et celle des formules chimiques.

Tableaux

Les tableaux sont utilisés pour présenter des données qui se répètent et devraient occuper le moins d'espace possible. Agencez les tableaux de façon qu'ils s'adaptent soit à une ou deux colonnes du Journal. Dactylographiez chaque tableau

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sur une page séparée et numérotez-les en chiffres arabes. Tracez des lignes horizontales de part et d'autre des en-têtes et au-dessous des colonnes, mais rarement ailleurs. N'utilisez jamais de lignes verticales. Laissez plutôt des espaces supplémentaires. Chaque tableau doit avoir une légende instructive, complète et indépendante. Les renvois des tableaux doivent être indiqués par des minuscules suscrites dactylographiées au bas du tableau. Placez les tableaux après la bibliographie. Notez que les *tableaux dans le texte* ne sont pas numérotés et sont dactylographiés dans le corps du texte. Ils ont rarement besoin de lignes horizontales.

Appendices

Les appendices doivent être indiqués de façon séquentielle (p. ex., A, B, C, etc.). Les illustrations et les tableaux en appendice doivent être numérotés différemment des illustrations et des tableaux du corps de l'article (p. ex., figure A1, tableau A1, etc.).

Documentation complémentaire

Le Conseil national de recherches du Canada administre un Dépôt des données non publiées dans lequel la documentation complémentaire peut être versée, à la demande des auteurs ou la directrice scientifique principale. De plus, il est maintenant possible d'accéder à cette documentation dans le format de son fichier d'origine à partir du site Web du Journal. L'accès se fera par le biais d'un hyperlien apparaissant dans la page Web de l'article pertinent. La documentation complémentaire peut comprendre de grands tableaux, des calculs complexes et des cartes détaillées qui ne sont pas essentiels à la compréhension ou à l'évaluation du document. Les auteurs qui désirent utiliser ce service doivent clairement indiquer les parties dont ils demandent le dépôt dès la soumission de leur article. Les tableaux et les figures doivent être numérotés de façon consécutive, distinctement de ceux destinés à la publication (p. ex., figure S1, tableau S1). Toute donnée déposée doit faire l'objet d'une note infrapaginale à la section appropriée du document. Des copies des données déposées peuvent être obtenues contre paiement auprès du Dépôt des données non publiées, ICIST, Conseil national de recherches du Canada, Ottawa, ON K1A 0S2, Canada.

Illustrations

Fournir des photographies, des imprimés laser (les imprimés par imprimante par points sont inacceptables) ou les dessins originaux (pourvu qu'ils ne dépassent pas 27,9 sur 43,2 cm (11 sur 17 po)) de chaque illustration. Transmettre trois copies des illustrations qui serviront au moment de la révision.

Chaque figure ou groupe de figures doit être préparé de manière à occuper, après une réduction appropriée, l'espace d'une ou deux colonnes du texte. Les dimensions finies maximales d'une illustration sur une colonne sont de 8,8 sur 23,9 cm (3,5 sur 9,4 po) et celles d'une illustration sur deux colonnes est de 18,2 sur 23,9 cm (7,2 sur 9,4 po). Les figures (y compris les similigravures) sont numérotées en chiffres arabes selon leur ordre séquentiel et doivent être annoncées dans le texte bien que tous leurs éléments doivent être intelligibles en eux-mêmes. Tous les termes, les abréviations et les symboles qui se trouvent dans les figures doivent être les mêmes que ceux apparaissant dans le texte. Seuls les détails essentiels devraient être identifiés; l'information plus détaillée devrait paraître dans la légende. Chaque illustration doit être identifiée, de préférence au bas, à gauche, par le numéro de la figure et les noms des auteurs, suffisamment éloignés de l'espace réservé à l'illustration.

Les **dessins au trait** originaux doivent être en encre noire ou produits par ordinateur en encre noire sur du papier blanc de première qualité ou un matériau comparable. Quant aux graphiques produits par ordinateur, il faut fournir un imprimé au laser de la meilleure résolution disponible. **Les photocopies ne sont pas acceptables.**

L'épaisseur des lignes doit être suffisante (au moins 0,5 point) pour que la reproduction soit nette; tous les symboles, les indices supérieurs ou inférieurs et les signes décimaux doivent être en bonne proportion avec le reste du dessin et suffisamment marqués pour permettre la réduction nécessaire sans perte de détail. Ne pas utiliser de petits symboles ouverts qui ont tendance à se refermer lorsqu'ils sont reproduits. **Le lettrage produit par imprimante à matrice de point ou par machine à écrire, ou à la main, ne sont pas acceptables.** Le même style de police et la même dimension de lettrage doivent servir dans toutes les figures de dimensions semblables d'un article.

Les **cartes** doivent avoir des motifs clairs et gras, et comporter les longitudes et latitudes (ou les coordonnées de Mercator transverses universelles) de même qu'une échelle graphique. Sur **les cartes du Québec**, les noms officiels des municipalités doivent être utilisés (p. ex., Québec, Montréal et Clarke City) et les entités géographiques doivent être présentées en français (p. ex., Lac Bienville), à l'exception de celles qui sont d'intérêt pancanadien — ces dernières, qui ont un nom officiel dans les deux langues (p. ex., Atlantic Ocean et océan Atlantique), se doivent de respecter la langue de l'article. Pour obtenir une liste complète des noms des régions d'intérêt pancanadien, consultez Le guide du rédacteur (p. 236–237, 2e éd., 1996), publié par les Travaux publics et Services gouvernementaux Canada, Ottawa, ON K1A 0S5, Canada.

Les **photographies** doivent être en *demi-teintes* sur papier glacé. Les épreuves doivent être de première qualité, sur papier glacé, avec contrastes bien marqués. Les copies destinées à la reprographie doivent être rognées de façon à ne laisser paraître que les éléments essentiels et être montées sur carton bristol blanc **léger** et flexible. Aucun espace ne doit paraître entre les photographies constituant une même planche. Une photographie ou un groupe de photographies doit être préparé de manière à occuper, **sans réduction supplémentaire**, une ou deux colonnes du texte. Les micrographies électroniques et les photomicrographies doivent comporter une échelle graphique à même l'illustration. On évitera les pertes de détails et de contraste inhérentes au procédé d'imprimerie en agençant le contraste et la densité de toutes les photographies montées sur une même planche.

Les **illustration en couleurs** sont aux frais de l'auteur. On peut obtenir de plus amples renseignements sur les prix auprès de Cecily Pearson, rédactrice administrative du Journal (613-993-9099; télécopieur : 613-952-7656; courriel : cecily.pearson@nrc-cnrc.gc.ca).

Les Presses scientifiques du CNRC préfèrent recevoir la version électronique des illustrations des manuscrits acceptés et l'utiliseront dans la mesure du possible. Si les fichiers électroniques ne sont pas disponibles, la version papier des illustrations sera balayée. Toutefois, le lecteur optique reproduit facilement les défauts (p. ex., le liquide correcteur, les maculations). Il est recommandé de ne pas soumettre de photographies tramées, ni des illustrations balayées imprimées au laser, à cause des moirures qui se forment; une moirure est un motif perceptible et non désiré produit par le rebalayage ou le retramage d'une illustration qui contient déjà un motif de points.

Préparation des fichiers électroniques des illustrations

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que des **originaux imprimés de haute qualité. Les fichiers électroniques (c.-à-d., le numéro et le contenu de la figure) doivent correspondre aux originaux imprimés.** Sur l'étiquette de la disquette, il faut indiquer (1) l'application et la version du logiciel; et (2) le(s) noms(s), la dimension et le suffixe du fichier. Si les fichiers ont été comprimés, il faut indiquer le format de compression. Les versions PC ou Macintosh des polices True Type ou Type 1 doivent être utilisées. **On ne doit pas se servir des polices de caractères en mode points ou non standard.** Les graphiques électroniques sont acceptés sur les disquettes suivantes : disquettes 3,5 po, cartouche Zip de 100 Mo et sur CD-ROM.

Le logiciel graphique préféré par les Presses scientifiques du CNRC est CorelDraw! Pour les autres applications possibles, reportez-vous à la « Liste des programmes graphiques électroniques » à http://pubs.nrc-cnrc.gc.ca/cgi-bin/rp/rp2_prog_ f?cjfas_graphics_f.html.

Toutes les illustrations doivent être soumises dans leur dimension de tirage final. Quant aux figures comportant plusieurs parties (p. ex., *a*, *b*, *c*, *d*, etc.) crées sur le même logiciel, elles doivent être assemblées dans un seul fichier plutôt que de transmettre plusieurs fichiers.

Il faut **garder** les illustrations le plus simple possible afin d'éviter les embûches. Éviter les textures et les fonds grisés compliqués, particulièrement dans les programmes d'illustration vectorielle.

Fichier en mode point — Les fichiers d'images en mode point sont produits sur une grille dans laquelle chaque carré (ou pixel) correspond à une nuance de noir, de couleur ou de gris. Un fichier en mode point est défini par le nombre de pixels ou d'éléments par pouce. Comme le pixel est défini comme un point, on parle aussi de « points par pouce » ou « ppp ». Plus la résolution de l'image est grande, plus le nombre de points sur une surface donnée est élevé.

Les illustrations soumises en mode point doivent être de définition adéquate. Les exigences minimales de définition sont les suivantes : 600 ppp pour les dessins au trait et les lignes fines (les dessins au trait comportant des lignes fines ou un fond grisé), 300 ppp pour les demi-teintes et les couleurs et 600 ppp pour les combinaisons (demi-teintes avec lettrage à l'extérieur de l'espace réservé à la photo).

Tous les fichiers en *couleurs* soumis doivent suivre la base CMJK (cyan, magenta, jaune et noir). Ces couleurs sont utilisées dans l'impression commerciale tout en couleur. Les graphiques RVB (le rouge, le vert et le bleu sont les couleurs utilisées particulièrement pour produire les images sur un écran) ne s'impriment pas correctement.

Fichiers vectoriels — Les fichiers vectoriels sont des fichiers d'images composées d'éléments comme les lignes et les formes. Ce type de fichier convient habituellement aux *dessins au trait*.

Fichiers vectoriels en mode point — Le mode points peut être importé dans un logiciel vectoriel ou de dessins aux seules fins d'ajouter et de superposer de l'information, des lignes, du texte, etc. Le mode points ne doit pas être redimensionné, recadré, tourné ou manipulé de toute autre façon après avoir été importé.

Conventions

Abréviations

N'abréger les termes désignant les unités de poids et mesures dans le texte que lorsqu'ils sont précédés d'un nombre.

becquerel (Bq)
calorie (cal)
centimètre (cm)
centimètre carré (cm^2)
centimètre cube (cm^3)
centimètres par gramme par seconde ($cm \cdot g^{-1} \cdot s^{-1}$)
coulomb (C)
décimètre (dm)
degré Celsius (°C)
degrés de liberté (dl)
écart type (ET)
électronvolt (eV)
erreur type (ErT)
farad (F)
gramme (g)
hectare (ha)
hertz (Hz)
heure (h)
joule (J)
kilomètre (km)
litre (L)
lumen (lm)
lux (lx)
mètre (m)
mètre carré (m^2)
mètre cube (m^3)
micromètre (μm)
milligramme (mg)
millilitre (mL)
millimètre (mm)
millimètre carré (mm^2)
minute (min)
masse molaire (M)
mole (mol)
moles par litre (mol/L, M)
pascal (Pa)
seconde (s)
tonne (métrique) (t)
volt (V)
volume (vol)
watt (W)

Dates

On écrira les dates dans l'ordre jour–mois–année, p. ex., 9 octobre 1983, sans virgule entre le mois et l'année.

Citations de références dans le texte

Système de nom et année

Le Journal utilise le système de nom et année, c.-à-d. que le nom de l'auteur ou des auteurs et l'année de publication sont insérés dans le texte à un endroit approprié : « Brown (1983) compare… » ou « …on a comparé (Brown 1983) ». Si la référence comporte plus de deux auteurs, inscrivez le nom du premier auteur seulement, suivi de « et al. » : « Brown et al. (1983) comparent… » ou « …on a comparé (Brown et al. 1983) ».

Communications personnelles

Les communications personnelles ne doivent pas être incluses dans la liste des références. Utilisez plutôt des parenthèses dans le texte, entre lesquelles vous indiquerez le nom et l'adresse de la personne en question, suivis de « communication personnelle ».

Données inédites

Si un livre ou un article inédit a été accepté pour publication, insérez-le dans la bibliographie, avec la mention « Sous presse ». On ne peut considérer comme étant sous presse que les manuscrits au stade d'épreuves ou ceux couverts par lettre d'acceptation. Si un article a été soumis mais n'a pas

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encore été accepté, ne l'incluez pas dans la liste de références, mais indiquez le nom et l'adresse de l'auteur du matériel inédit, dans le texte lui-même, avec la mention « données inédites ».

Bibliographie

Les références doivent être classées par ordre alphabétique des noms des premiers auteurs. Si la liste comprend plusieurs publications d'un même premier auteur, les règles suivantes seront appliquées. (1) S'il n'y a qu'**un auteur**, les ouvrages se succèdent par ordre chronologique de partition en commençant par le plus ancien. Si l'auteur a publié, au cours d'une année, plusieurs livres ou articles, on distinguera les références les unes des autres en faisant suivre l'année de publication d'une lettre (*a*, *b*, *c*, etc.). (2) S'il y a **deux auteurs**, les ouvrages sont placés à la suite de ceux n'ayant qu'un auteur, et sont alors classés par ordre alphabétique du nom du deuxième auteur. (3) S'il y a **trois auteurs ou plus**, les ouvrages sont placés à la suite de ceux ayant deux auteurs et sont classés par ordre chronologique.

La liste qui suit donne des exemples de ponctuation, de style et d'abréviations utilisés dans les références bibliographiques (d'après *CASSI* ou *BIOSIS® Serial Sources*).

Article d'une revue

Archambault, D., et Bourget, E. 1983. Importance du régime de dénudation sur la structure et la succession des communautés intertidales de substrat rocheux en milieux subarctiques. Can. J. Fish. Aquat. Sci. **40** : 1278–1292.

Numéro complet d'une revue

Gordon, D.C., Jr., et Hourston, A.S. (*Directeurs de la rédaction*). 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. **40**(suppl. 1).

Livre dans une série

Scott, W.B., et Crossman, E.J. 1974. Poisons d'eau douce du Canada. Bull. can. sci. halieut. aquat. n° 184.

Livre ne faisant pas partie d'une série

Forrester, W.D. 1983. Manuel canadien des marées. Service hydrographique du Canada, ministère des Pêches et des Océans, Ottawa.

Partie d'un livre

Aubert, M., Aubert, J., Daniel, S., et Desirotte, N. 1982. État actuel de la pollution bactérienne au large des côtes françaises. *Dans* La pollution des mers et les ressources biologiques. *Sous la direction de* M. Ruivo. Fishing News (Books) Ltd., Londres. p. 36–40.

Corporation auteur

American Public Health Association, American Water Works Association et Water Pollution Control Federation. 1975. Standard methods for the examination of water and wastewater. 14e éd. Washington.

Thèse

Delisle, C. 1969. Écologie, croissance et comportement de l'éperlan du Lac Heney, Comté de Gatineau ainsi que la répartition en eau douce du Québec. Thèse de doctorat, Université d'Ottawa, Ottawa.

Rapport

Dutil, D.J., Fortin, M., et Vigneault, Y. 1982. L'importance des zones littorales pour les ressources halieutiques. Mémoire remis au Conseil consultatif de l'environnement du Québec. Rapp. manuscrit can. sci. halieut. aquat. n° 1653.

Traduction

Koike, A., et Ogura, B. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. **64** : 1–11. [Traduit du japonais par Can. Transl. Fish. Aquat. Sci. n° 4950, 1983.]

Liste de mots

Cette section, dans la version anglaise du Guide, contient une série de mots dont l'orthographe pose certains problèmes d'uniformité, comme, p. ex., « cold water » (nom) « coldwater » (adjectif); « hard water » (nom) « hardwater » (adjectif), etc. L'auteur préparant un texte en anglais est prié de consulter la version anglaise du Guide.

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